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Torrey Botanical Club

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BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 79, NO. 6, pp. 427–430 NOVEMBER, 1952

VITAMIM B_1 REQUIREMENT OF RUMEX VIRUS TUMOR TISSUE

LOUIS G. NICKELL

In the first detailed report concerning the growth *in vitro* of the virus tumor from sorrel, *Rumex acetosa* (Burkholder and Nickell 1949), it was stated that there was no apparent vitamin requirement in the tumor tissue. This statement was based on observations of tissue grown on a vitamin-free basal medium for only one transfer. However, the tumor tissue is from the root portion of the sorrel plant, and no root or root tissue has so far been grown indefinitely *in vitro* without an external supply of vitamin B_1 (White 1943). There are two papers in the literature wherein roots have been reported to synthesize this vitamin (Bonner and Devirian 1939, McClary 1940.). Therefore, it was thought worthwhile to investigate further the vitamin utilization by this tissue, i.e., experiments designed to cover two or more consecutive transfer periods.

Preliminary experiments showed that growth of the tissue on a vitamin-free synthetic medium for the first transfer was the same as, or slightly less than, that of tissue grown on the same medium with added vitamins (B_1, B_6, and niacinamide). However, if this same tissue was then transferred to the vitamin-free medium for a second growth period, the growth rate dropped precipitously, or the tissue died. No tissue survived a third transfer. These results strongly indicated a vitamin requirement, and prompted the following experiments.

Material and methods. The material and methods used in the present study are essentially the same as those used previously (Burkholder and Nickell 1949, Nickell 1950a and b, 1951, Nickell and Burkholder 1948, 1950). The tissue used was the R_1 strain of the virus tumor isolated by Black (1947), and the synthetic basal medium used throughout was No. 24 with or without added vitamins (Burkholder and Nickell 1949). The experimental growth period in all instances was three weeks. All values presented are based on at least 5 replicates for a given set of conditions.

Experimental results. Omission series. Since the preliminary experiments indicated that this tissue requires one or more vitamins for growth, experiments were set up with the three vitamins (B_1, B_6 and niacinamide) omitted singly, and all together. The tissue used in these experiments was grown, prior to the experimental transfer, on the basal medium plus all three vitamins. The growth values after the first experimental transfer show a slight drop in those media from which vitamin B_1 was omitted. In the remaining media the growth values are normal (table 1).

[THE BULLETIN for September–October (79: 351–425) was issued August 22, 1952]

TABLE 1. *Vitamin requirement of Rumex virus tumor tissue—Omission series (experimental transfers grown on medium with all three vitamins present prior to experiment)*

Vitamins	+ = vitamin added − = vitamin omitted				
B_1	+	−	+	+	−
B_6	+	+	−	+	−
Niacinamide	+	+	+	−	−
First transfer	5.4*	3.5	5.5	5.4	3.3
Second transfer A	5.5	dead	6.0	5.0	dead
Second transfer B	6.3	dead	5.6	5.5	dead

* Numbers express growth value.
growth value = final wet weight/initial wet weight.

The tissues from this first transfer were used for the second transfer, being placed on the same type medium on which they had grown previously. The results (table 1) show that all tissues grown in the absence of vitamin B_1 for two successive transfers have died. All others have continued at the same growth rate. The second transfer was done in duplicate sets of experiments, and the results are quite consistent. The evidence indicates that vitamin B_1 and B_1 alone is required for growth by this tissue.

Addition series. In order to check on the requirement for vitamin B_1, tumors were grown on the basal medium without any vitamins, and after one month's growth were placed on the basal medium alone or with the addition of one or more vitamins as indicated in table 2. The results here show clearly that vitamin B_1 is the only one required for growth.

Concentration series. Since the tissue has been maintained on the basal medium with 0.1 ppm of vitamin B_1 (plus other vitamins) for over 6 years, a concentration series was set up in order to determine if this is the optimal level. The tissue to be used for this experiment was first grown for one month on the basal medium without the addition of vitamins; transfers then are made to media containing vitamin B_1 from 0 to 0.4 ppm. The results, presented in figure 1, show that the amount used previously is somewhat low for optimal growth.

Indefinite culture with vitamin B_1 alone. While the evidence presented

TABLE 2. *Vitamin requirement of Rumex virus tumor tissue—Addition series (experimental transfers grown on vitamin free medium for one month prior to experiment)*

Vitamins	+ = vitamin added − = vitamin omitted							
B_1	+	−	+	+	−	−	+	−
B_6	+	+	−	+	−	+	−	−
Niacinamide	+	+	+	−	+	−	−	−
	5.4*	dead	6.5	5.1	dead	dead	6.4	dead

* Numbers express growth value.

indicates that vitamin B_1 is the only vitamin required for growth of the *Rumex* virus tumor tissue, absolute proof would be provided if the tissue were to be grown in the absence of all other vitamins for an extended period of time. This has been done. At the present time, tissue of this tumor has been maintained for over two years, with sub-culturing every three weeks, on the basal medium plus vitamin B_1 at a level of 0.1 ppm and no other vitamins. Growth has been normal in every respect and exactly like that of sister cultures maintained on the basal medium plus all three vitamins (B_1, B_6 and niacinamide).

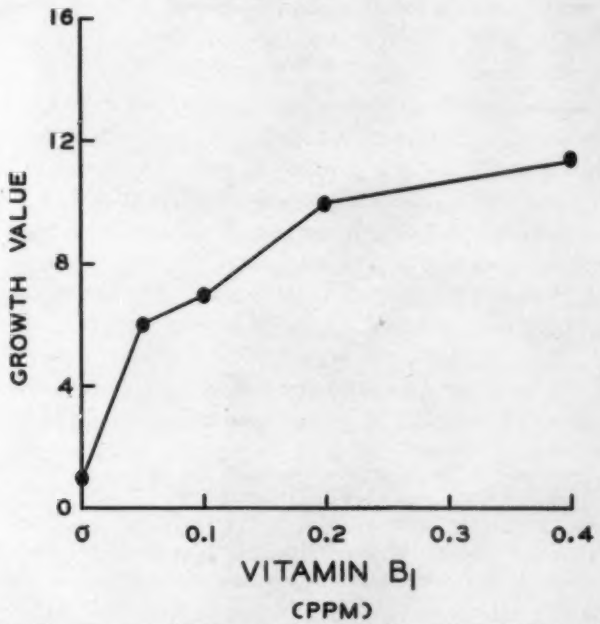

FIG. 1. Growth response of *Rumex* virus tumor tissue to additions of vitamin B_1 to the basal medium (No. 24).

Discussion. The results presented in this paper show that the formation of a tumorous condition in sorrel root tissue has in no way changed the vitamin B_1 nutrient requirement that is characteristic of roots which have been grown indefinitely *in vitro*.

Other nutritional studies with this tissue have shown that there are differences between normal excised roots and virus tumors of sorrel. The virus tumor has an abnormally high phosphate requirement (Nickell and Burkholder 1948, Burkholder and Nickell 1949) while uninfected excised roots have a normal requirement (unpublished data). Studies concerning the effects of nucleic acid derivatives and related compounds on the growth of the virus tumors showed hypoxanthine to be stimulatory (Nickell, Greenfield and Burkholder 1950). This compound has no stimulatory effect on the

growth of excised roots of sorrel at the same concentrations used in the studies with the tumors (unpublished data). Experiments employing lower concentrations of hypoxanthine are in progress.

Two differences between the normal and neoplastic tissues of sorrel have been discussed (phosphate and hypoxanthine), neither of which is incompatible with the hypothesis that the difference could be due to an effect of the virus requirements superimposed on the normal metabolism of the host tissue. Stimulatory effects by increased phosphate and/or the presence of certain purines or pyrimidines could well be due to the increased demand for them for incorporation into virus nucleoprotein.

SUMMARY

1. It has been shown that virus tumor tissue from the root of the sorrel plant (*Rumex acetosa* L.) requires vitamin B_1 for growth *in vitro*, and no other vitamin.

2. This requirement has been demonstrated by an omission series of experiments, an addition series, and continued growth for over two years on the basal synthetic medium plus vitamin B_1.

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BULLETIN OF THE TORREY BOTANICAL CLUB

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PRODUCTION OF ZOOSPORES FROM GERMINATING OOSPORES OF PYTHIUM ULTIMUM AND PYTHIUM DEBARYANUM[1]

CHARLES DRECHSLER[2]

Seventy years ago de Bary (1881b, p. 525) described oospores of *Pythium debaryanum* Hesse as germinating, after a resting period of 4 to 5 months, by production of a germ hypha, which in pure water devoid of nutrients would grow out and ramify rather considerably before it eventually died off in forming a resting conidium. If the germ hypha reached a favorable substratum it formed an extensive mycelium capable of normal reproduction. It was not seen giving rise to zoosporangia. De Bary's (1881 a, p. 12–14, Taf. I, figs. 9a, 10–13, 14b, 16–19; 1881 b, fig. 1) detailed account of the developmental morphology of the antheridium in *P. debaryanum*—the manner of origin of this organ, its shape, and its most usual positional and postural relationships to the oogonium—indicates that his studies on the formative and mature stages of sexual reproduction very probably were carried out for the most part on material of the exceedingly widespread damping-off parasite which on grounds set forth earlier (Drechsler 1927, 1935) seems best referable to *P. ultimum* Trow. Yet as the damping-off fungus best conforming to the figures of sporangia and sexual reproductive apparatus that are given in the original account of *P. debaryanum* (Hesse 1874, figs. 5–9, 11, 13, 14) is likewise ubiquitous and abundant in moist temperate lands, often, indeed, occurring together with *P. ultimum*, it could presumably have also been present in addition to the 6 other much less frequent congeneric species de Bary found growing out of affected garden cress (*Lepidium sativum* L.) seedlings. Assuredly the zoospore development which de Bary ascribed to *P. debaryanum* and which puzzled him by its pronounced inconstancy—some cultures producing rather many functional zoosporangia while others produced none—could more readily have come from an admixture of the species named in his honor than from the parasite whose sexual development he so accurately described. It seems therefore not altogether impossible that the single germinating oospore he figured without an attached empty antheridium (de Bary 1881b, fig. 2) may really have belonged to Hesse's species, though, again, it may with at least equal probability have belonged to *P. ultimum*. When Trow (1901) twenty years later described *P. ultimum* as a new species he set forth its oospores as germinating

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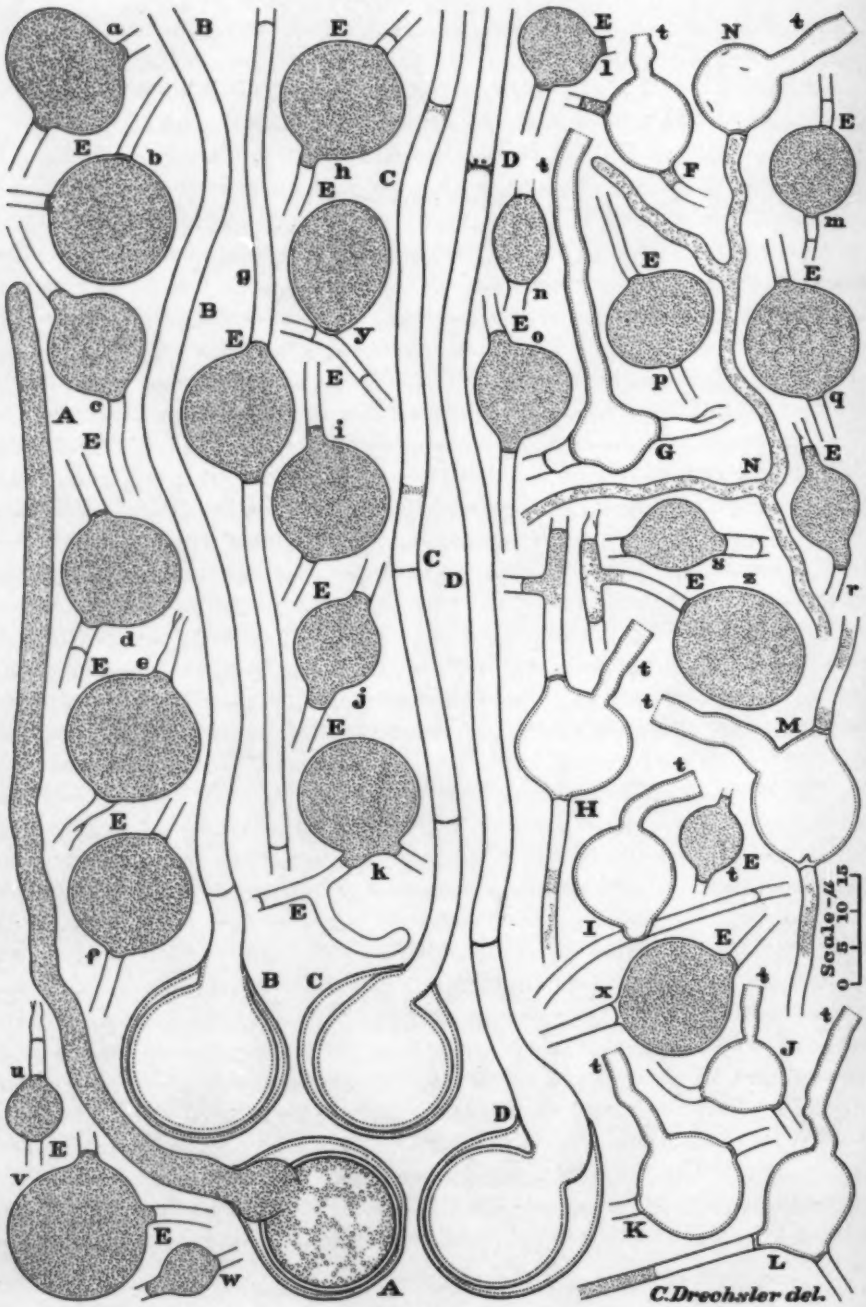
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always by the production of one or more germ tubes, either soon after reaching maturity or after they had rested for a variable period extending up to 7 months.

The commonplace vegetative germination ascribed by de Bary to the oospores of *Pythium debaryanum* and by Trow to those of *P. ultimum* can be achieved readily and abundantly in these 2 species at the temperatures ordinarily prevailing in most American laboratories. Maizemeal-agar plate cultures of either species containing in suspension some finely divided maizemeal will usually show rapid mycelial growth, copious sexual reproduction, and subsequently gradual after-ripening of oospores, not only in summer when indoor temperatures fluctuate commonly between 25° and 33° C., but also in winter when rooms are kept heated to temperatures ranging from 22° to 28° C. To insure this sequence of development it is necessary only to keep the cultures from drying out—a matter easily accomplished by placing them in stacks under bell-jars or inverted battery jars. If after such storage for a period of 2 to 4 months, portions of agar are removed to a shallow layer of pure water, many of the oospores will germinate promptly at ordinary laboratory temperature by putting forth a germ hypha (fig. 1, A–D) capable of extensive mycelial growth.

As has been made known in a preliminary report (Drechsler 1946a) more distinctive germination by production of motile zoospores ensues when after-ripened oospores of *Pythium debaryanum* or of *P. ultimum* are transferred to pure water at lower temperatures. This type of germinative development is of moment especially in the case of *P. ultimum*, since this species generally displays very little inclination, even under chilly conditions, to produce zoospores from its ordinary asexual conidia. All pure cultures so far tried out, which from the character of their mycelium and the morphology of their sexual reproductive apparatus could be referred to *P. ultimum*, have proved reluctant to form zoospores from their conidia of mycelial origin, while showing much readiness and consistency in producing them from their after-ripened oospores. The figures herein given to illustrate the formative and germinative phases of oospore development in Trow's species were prepared mainly from 2 cultures obtained as manifest causal agents in separate instances of plant disease recorded in earlier papers. Of these 2 cultures one (fig. 2, A–M; fig. 3, A–J) was isolated in 1924 from a cabbage (*Brassica oleracea* L. var. *capitata* L.) head affected with stump rot

FIG. 1. *Pythium ultimum*, drawn to a uniform magnification with the aid of a camera lucida; × 1000 throughout. A, after-ripened oospore germinating by production of a germ tube. B–D, Oospore envelopes, each with empty proximal portion of a long vegetative germ hypha. E, Small conidia or zoosporangia, a–z, formed on germ hyphae. F–N, Empty envelopes of such small zoosporangia that have discharged their contents through the evacuation tube, t, for conversion into zoospores. (A–D, M, N, drawn from sweet-potato strain; E (a–z), F–L, drawn from cabbage strain.)

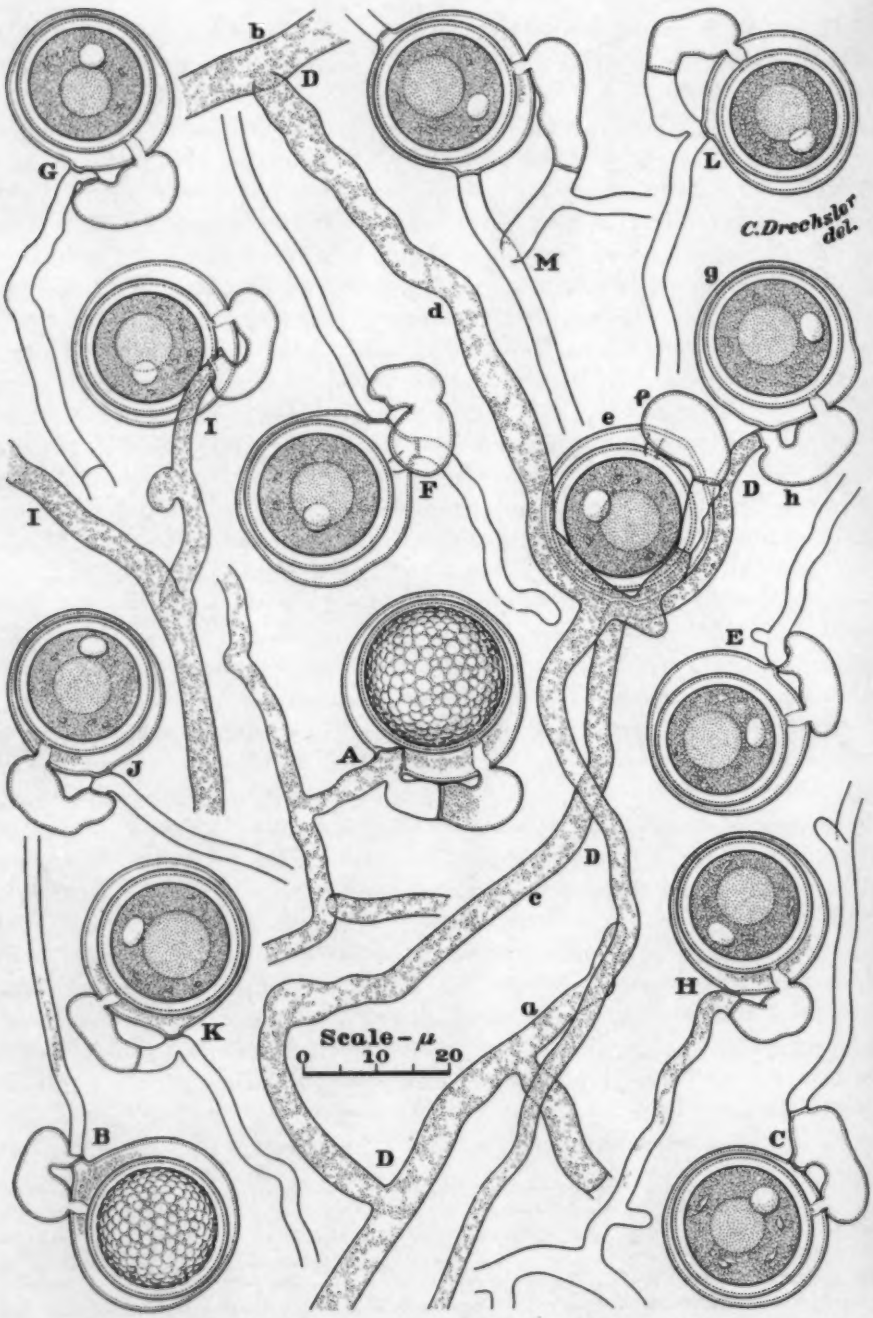
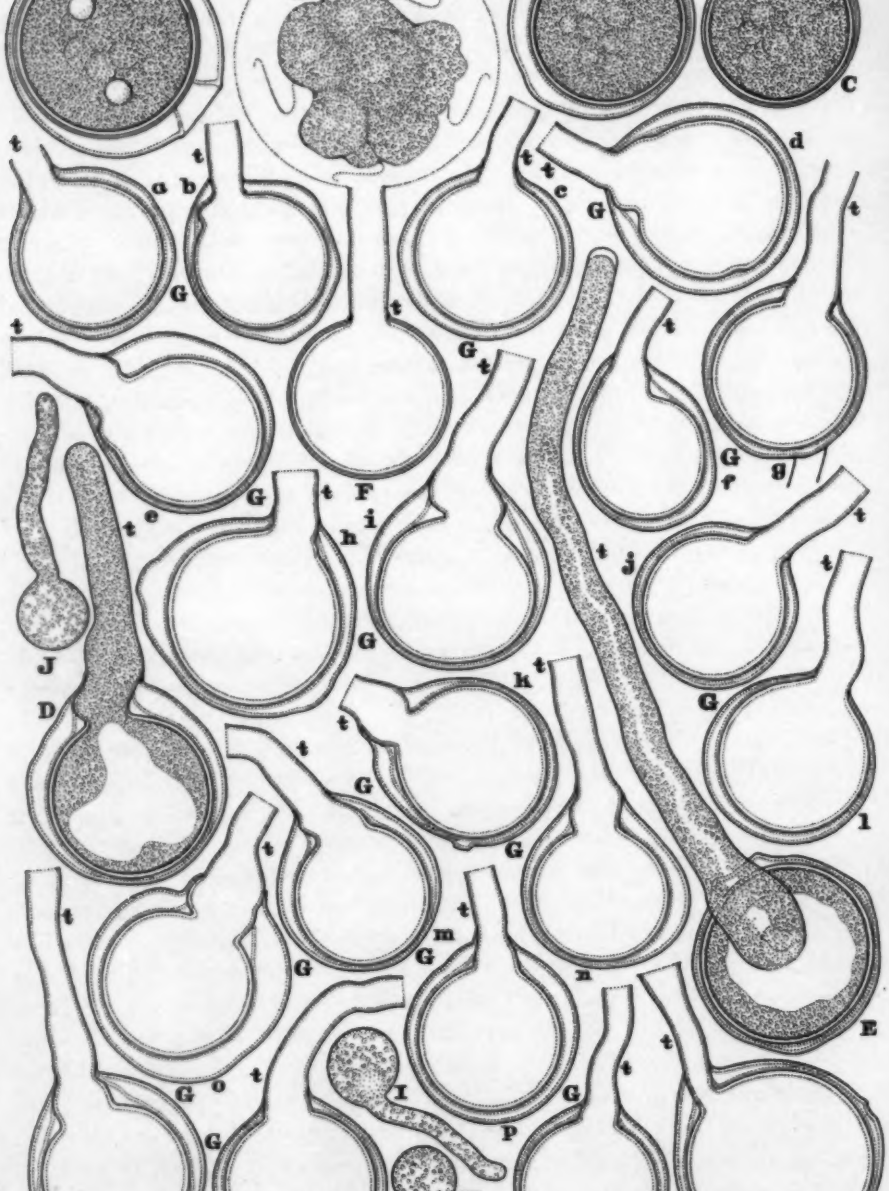


FIG. 2. Sexual reproductive apparatus of *Pythium ultimum* (cabbage strain) drawn with the aid of a camera lucida, at a uniform magnification, from the underside of maizemeal-agar plate cultures; ×1000 throughout. Explanation of all parts given in text.

(Drechsler 1925), while the other (fig. 4, A–O; fig. 5, A–Z) was received the same year from L. L. Harter, who had isolated it from a darkened rootlet of a sweetpotato (*Ipomoea batatas* (L.) Lam. var. Red Brazil) slip in the spring of 1924 (Harter 1925). Occasion is taken to include also a few supplementary drawings of conidia and sexual reproductive apparatus that were prepared from 2 cultures labelled "G 5" (fig. 6, A–G) and "G 3" (fig. 6, H–M), respectively, which Harry Braun kindly gave me in February, 1925, as being representative of forms he had isolated from decaying geranium (*Pelargonium* sp.) cuttings and had treated separately under the names *P. debaryanum* and *P. debaryanum* var. *pelargonii* in a paper that was published some months later (Braun 1925). Both of Braun's cultures were clearly referable to *P. ultimum* as that species is understood here and were wholly alien to Hesse's species. Several units of sexual apparatus (fig. 6, N–R) drawn from a culture isolated from a partly decayed geranium cutting in a greenhouse near Cedarville, N. J., on May 29, 1924, likewise reveal the make-up characteristic of *P. ultimum*, as do also 3 additional units (fig. 6, S–U) drawn from 3 separate cultures isolated originally from separate collections of softened pea (*Pisum sativum* L.) roots. Of the 3 pea-root collections one was made near Onalaska, Wis., in the spring of 1922 (fig. 6, S), another near Salt Lake City, Utah, on August 20, 1923 (fig. 6, T), and the third in Arlington, Va., on June 9, 1921 (fig. 6, U). A culture originally isolated from a softened pea root taken from a field near Rochelle, Ill., on June 12, 1924, was used in preparing the figures relating to sexual reproduction (fig. 7, A–T) and oospore germination (fig. 8, A–V) in *P. debaryanum*.

The oogonia of *Pythium ultimum* are borne either terminally (fig. 6, A, I–K, N–P, R, S) or intercalarily (fig. 6, B–D, H, Q, T, U). Their position in considerable degree seems to be governed by the width of their supporting hyphae. On the under side of agar plate cultures, where mycelial filaments are relatively narrow, the female cell is formed terminally (fig. 2, A–C; D, g; E; G–L) more often than in subterminal (fig. 2, F) or intercalary (fig. 2, M) positions. Units of sexual apparatus produced by the wider hyphae abundant on the upper side of a maizemeal-agar plate culture commonly show the oogonium in an intercalary position (fig. 4, A; B; D, a; F–H; K; L, a; M–O), though here and there a stout hypha may bear an oogonium terminally (fig. 4, C) or laterally (4, D, b). Slender hyphae on the upper surface of an agar plate culture will, as elsewhere, most often give rise to oogonia terminally (fig. 4, E, b; J) or subterminally (fig. 4, I). Now and then an oogonium that was formed terminally (fig. 2, D, e; fig. 4, E, b) comes to occupy an approximately lateral position when the supporting hypha grows out below the basal septum, often to produce a second oogonium (fig. 2, D, g; fig. 4, E, a) some distance forward.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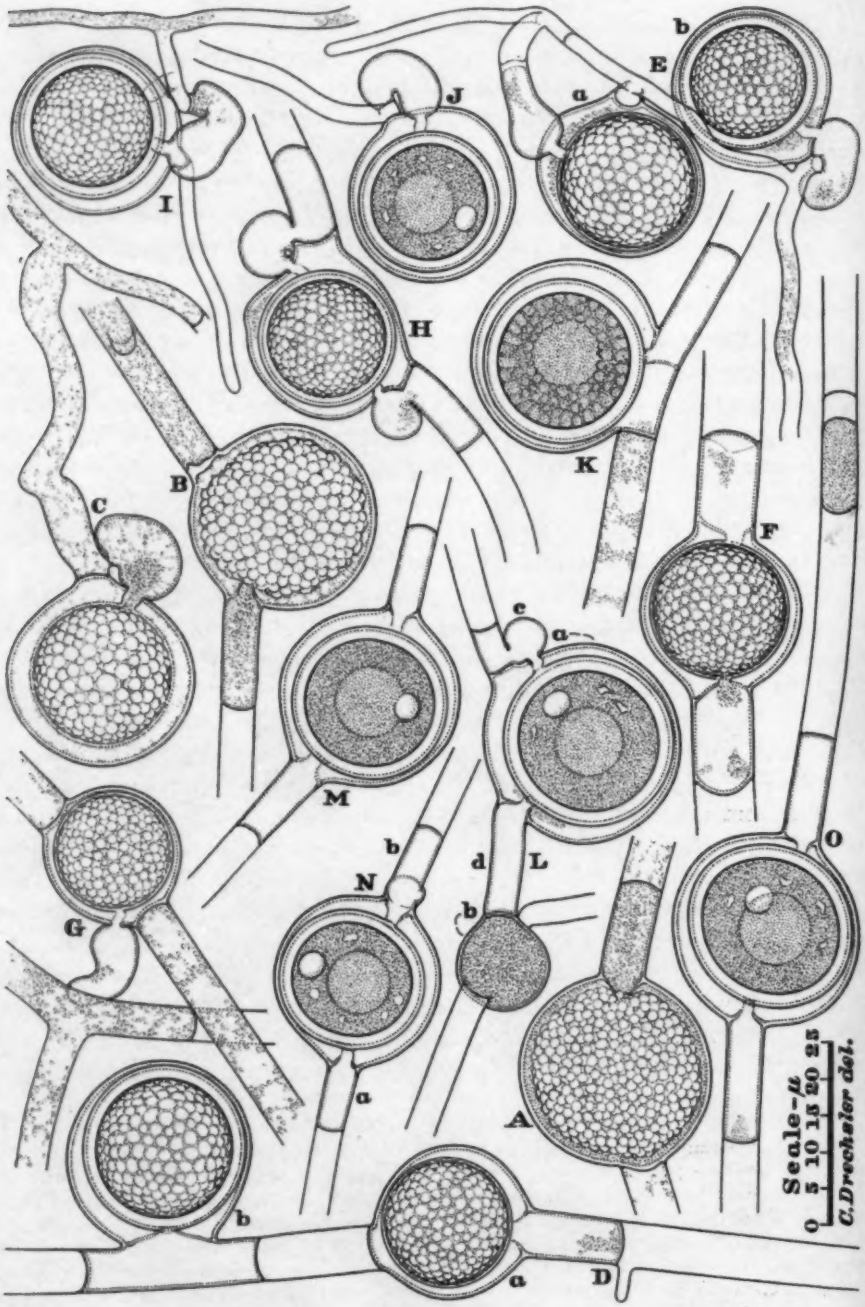
The width of the supporting filament affects also the position and shape of antheridia in monoclinous units of sexual reproductive apparatus. Where a wide filament bears an intercalary oogonium, fertilization is accomplished often by a single antheridium that consists merely of an adjacent cylindrical hyphal segment (fig. 4, A; B; D, a; K. fig. 6, Q). Frequently, again, a male cell of unmodified cylindrical shape is delimited at each pole of the oogonium (fig. 4, F, M, O; fig. 6, D, a, b), though often when 2 adjacent antheridia are present one of them may be of plain cylindrical shape (fig. 4, L, d; N, a. fig. 6, T, a), while the other is modified by a protrusion close to the oogonium (fig. 4, L, c; N, b. fig. 6, T, b), or each of the two may have a bulbous protrusion (fig. 4, H). Adjacent antheridia of unmodified cylindrical shape always extend their fertilization tube through the cross-wall delimiting them from the oogonium, and this is true also of some antheridia which have only a rather small lateral protrusion (fig. 4, N, b). Where the protrusion is fairly large the fertilization tube is usually pushed through the subspherical envelope of the oogonium in a position not far from the cross-wall (fig. 4, H; L, c. fig. 6, T, b). In monoclinous units of sexual apparatus that are borne terminally on rather slender hyphae an adjacent antheridium often consists of a small hyphal part together with a lateral protuberant part many times larger (fig. 2, B; C; D, h; I. fig. 6, A, I, K, O, P, S). Very often, too, in such terminal monoclinous units the antheridium includes no hyphal part at all, but is derived entirely from the lateral outgrowth. The whole outgrowth may be included in the antheridium, so that this organ appears as a plump arched body sessile on the supporting hypha (fig. 2, E, F; fig. 4, C, J; fig. 6, H. N); or a proximal portion of the outgrowth, sometimes very short (fig. 2, G, H, J. fig. 4, E, b; I) but at other times longer (fig. 2, A, K, L), may serve as a stalk terminally supporting the curved male cell.

Development of an antheridium largely or wholly from a lateral outgrowth extended from a position immediately below the basal septum of a terminal oogonium often brings the oogonium markedly out of alignment with its supporting hypha. In water preparations, as de Bary (1881a, p. 14) noted, and similarly in very soft gel substrata, the antheridium, though originating laterally below the terminal oogonium, will tend so strongly to

---

FIG. 3. Germination of oospores from 90-day-old maizemeal-agar plate cultures of *Pythium ultimum* (cabbage strain); all parts drawn to a uniform magification with the aid of a camera lucida; × 1000 throughout. A, B, After-ripened oospores. C, After-ripened oospore beginning to germinate. D, Oospore with elongating germ tube, t. E, Oospore with unusually long germ tube, t, surmounted by a cap of dehiscense. F, Oospore that has discharged its contents through the evacuation tube, t, into the vesicle, v, where they are being fashioned into zoospores. G, Empty membranous envelopes (a–s, u) of oogonium, oospore, and evacuation tube, t, remaining after escape of zoospores. H, Encysted zoospore. I, J, Encysted zoospores, each putting forth a germ tube.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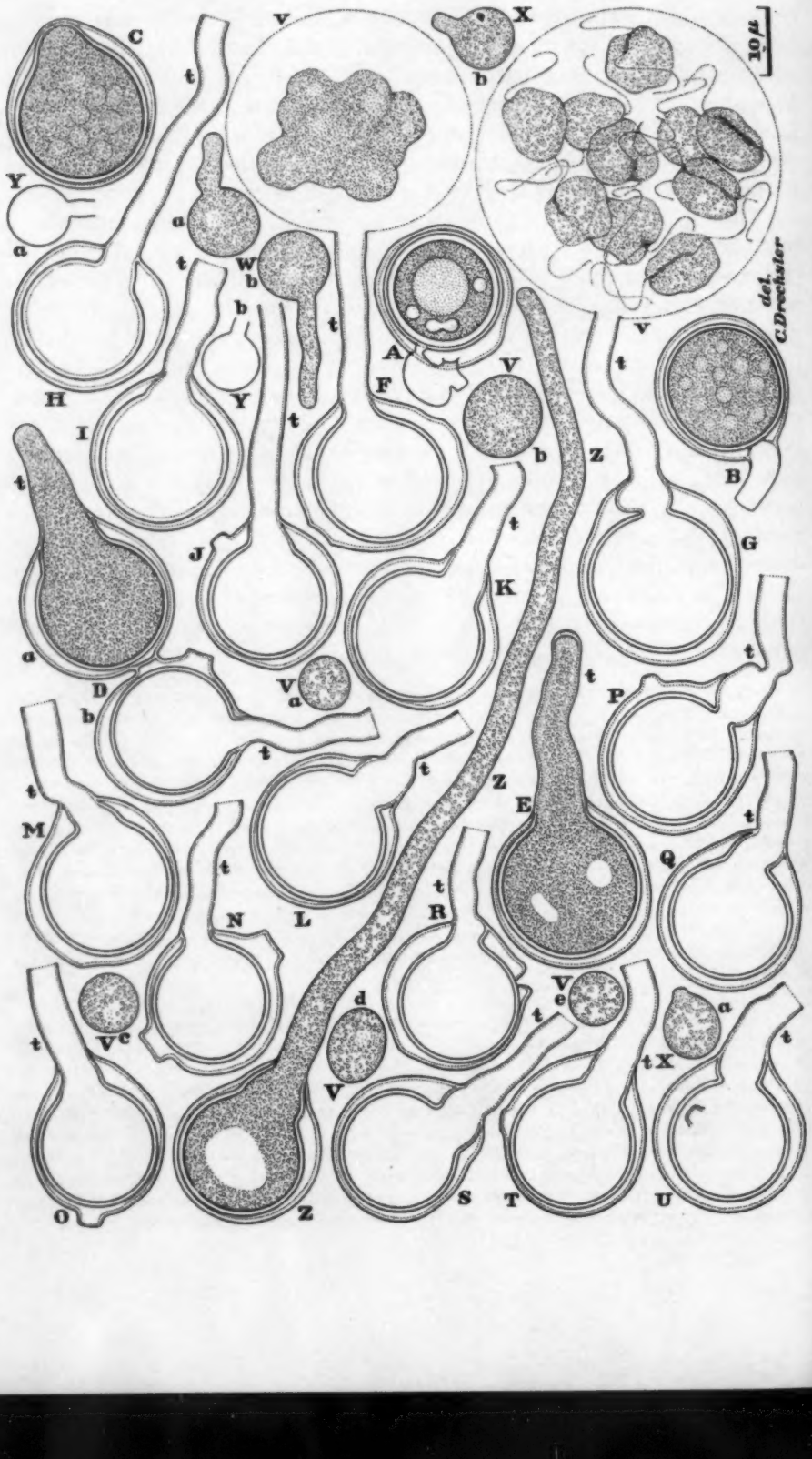
grow straightforward that the oogonium is pushed aside and may come to lie at a right angle with the supporting hypha. In moderately firm agar cultures, where massive parts cannot move freely in response to growth pressures, displacement of the oogonium is impeded, though some approximation to the angular relationships observable in irrigated material may come about here through rather abrupt bending of the distal portion of the supporting hypha (fig. 2, B; D, g, h. fig. 6, I, P, S).

Although the sexual reproductive apparatus of *Pythium ultimum* is predominantly monoclinous, units of diclinous origin are not infrequent in the species. Sometimes two mycelial filaments (fig. 2, D, a, b) rather far apart give off long branches (fig. 2, D, c, d) on which the oogonium (fig. 2, D, e) and the antheridium (fig. 2, D, f) fertilizing it are borne terminally, the male cell then usually being of curved clavate shape. In instances where the two mycelial filaments supplying the apposed organs are closer together, the antheridium may be formed on a short stalk (fig. 6, R) or may be borne laterally and sessile as a straight or somewhat curved, elongated utriform structure (fig. 4, G). Most often when the male hypha lies close to the oogonium, the antheridium consists of an intercalary segment of the hypha together with a protuberant part (fig. 6, B; D, c; T, c) in somewhat broad contact with the oogonium—a make-up more or less suggestive of the antheridia in *P. butleri* Subr. and *P. aphanidermatum* (Eds.) Fitzp.[2] Sometimes an intercalary antheridium of diclinous origin will have 2 protuberant parts, each of them provided with a fertilization tube (fig. 6, C).

[2] These 2 closely related species, which were adjudged to be identical by Carpenter (1921) and Fitzpatrick (1923) though apparently neither author had studied material referable to either species, are distinguished here on grounds set forth briefly in an abstract (Drechsler 1934). My examination of Dr. Edson's excellent microscope mounts, together with the adverse comments he made when on various occasions during the 5 years following 1922 he kindly examined maizemeal-agar plate cultures and irrigated preparations of the larger, strongly lobulated species, gave good reason for holding that his description (Edson 1915) was based on the smaller, often rather meagerly lobulated species which soon afterwards came to light in 3 cultures that R. D. Rands isolated from sugarcane roots in Louisiana. Since these cultures were found unmistakably conspecific with 2 Sumatra cultures that represented the same stem-burn parasite—the "*Pythium debaryanum*" of Jochems (1927)—on which Meurs (1934) based his description of *P. deliense*, it would seem that *P. aphanidermatum* has a synonym in *P. deliense* rather than in *P. butleri*.

FIG. 4. Sexual reproductive apparatus of *Pythium ultimum* (sweet-potato strain) drawn with the aid of a camera lucida, at a uniform magnification, from the upper side of maizemeal-agar plate cultures; ×1000 throughout. A, B, Oogonia being fertilized by adjacent antheridia. C, Fertilized oogonium showing young oospore with thin wall. D, E, Portions of hypha, each with two oogonia, whereof one, a, shows an oospore with very thin wall, while the other, b, contains an oospore with a thicker wall. F, G, Oogonia, each with a young thin-walled oospore. H, I, Oogonia containing oospores with thicker walls. J, Mature monoclinous sexual reproductive unit. K, Somewhat immature monoclinous unit. L, Portion of hypha with oogonium, a, and conidium, b; the former having been fertilized by two antheridia, c and d. M–O, Mature monoclinous sexual units.


10 μ
del. C. Drechsler

Such production of 2 fertilization tubes, instances of which are also observable now and then in monoclinous lateral antheridia that arise in immediate proximity to the oogonium, may be regarded as exceptional. Departures from the more usual trends of development result in miscellaneous variations. In monoclinous terminal reproductive units, for example, the adjacent antheridium, usually of cylindrical shape, sometimes widens markedly toward the broad base of the oogonium (fig. 6, J), its conformation then representing a frustrum of an inverted cone. Occasionally, again, in monoclinous apparatus a lateral (fig. 4, E, a) or an intercalary (fig. 2, M) oogonium may be found supplied, as in *P. debaryanum*, with an antheridium borne on a short branch arising 10 to 15 μ away. In scattered instances an oogonium formed laterally on a wide hypha will, on conversion of the adjoining portion of the hypha into a male cell, come to be sessile on an intercalary antheridium (fig. 4, D, b).

Development within the oogonium follows the course usual in members of the genus. At the time of fertilization the protoplasmic mass is drawn away from the oogonial envelope (fig. 4, A, B). After the antheridium has contributed most or all of its granular contents, the fertilized protoplast assumes a more accurately spherical shape and lays down a thin colorless peripheral membrane (fig. 4, C; D, a; E, a; F; G). The coarsely lumpy protoplasmic mass now undergoes some little further contraction as it secretes a second wall layer thicker than the first (fig. 2, A; B. fig. 4, D, b; E, b; H; I). A homogeneous reserve globule appears in the center of the young oospore, its progressive enlargement constraining the lumpy mass into a parietal layer (fig. 4, K). Thereupon when the lumps become resolved into small granules, and a single subspherical or slightly flattened refringent body emerges clearly in the granular material, the oospore reaches its fully mature resting condition (fig. 2, C; D, e, g; E–M. fig. 4, J; L, a; M–O. fig. 6, A–D; H–K; N–U). In this condition the oospore regularly fails to germinate when it is placed in pure water. During prolonged storage at a low temperature—at 5° C., for example—such dormant oospores reveal

FIG. 5. Germination of oospores from 90-day-old maizemeal-agar plate cultures of *Pythium ultimum* (sweetpotato strain); all parts drawn to a uniform magnification with the aid of a camera lucida; ×1000 throughout. A, Oospore in early stage of after-ripening. B, After-ripened oospore. C, Oospore beginning to germinate. D, two adjacent oogonia, a and b; from the oospore in the oogonium, a, the germ tube, t, has grown out; the oospore in oogonium, b, has emptied out its contents through the evacuation tube, t. E, Oospore with germ tube surmounted by cap of dehiscense. F, Discharged oospore; t, evacuation tube; v, vesicle with protoplasmic mass undergoing cleavage. G, Discharged oospore; t, evacuation tube; v, vesicle with ten full-fledged zoospores. H–U, Empty envelopes of oogonium, oospore, and evacuation tube, t. V, Encysted zoospores, a–e. W, Encysted oospores, a and b, germinating vegetatively. X, Encysted zoospores, a and b, each with papilla of dehiscense. Y, Zoospore cyst envelopes, a and b, after escape of secondary motile zoospore. Z, Oospore with long vegetative germ hypha.

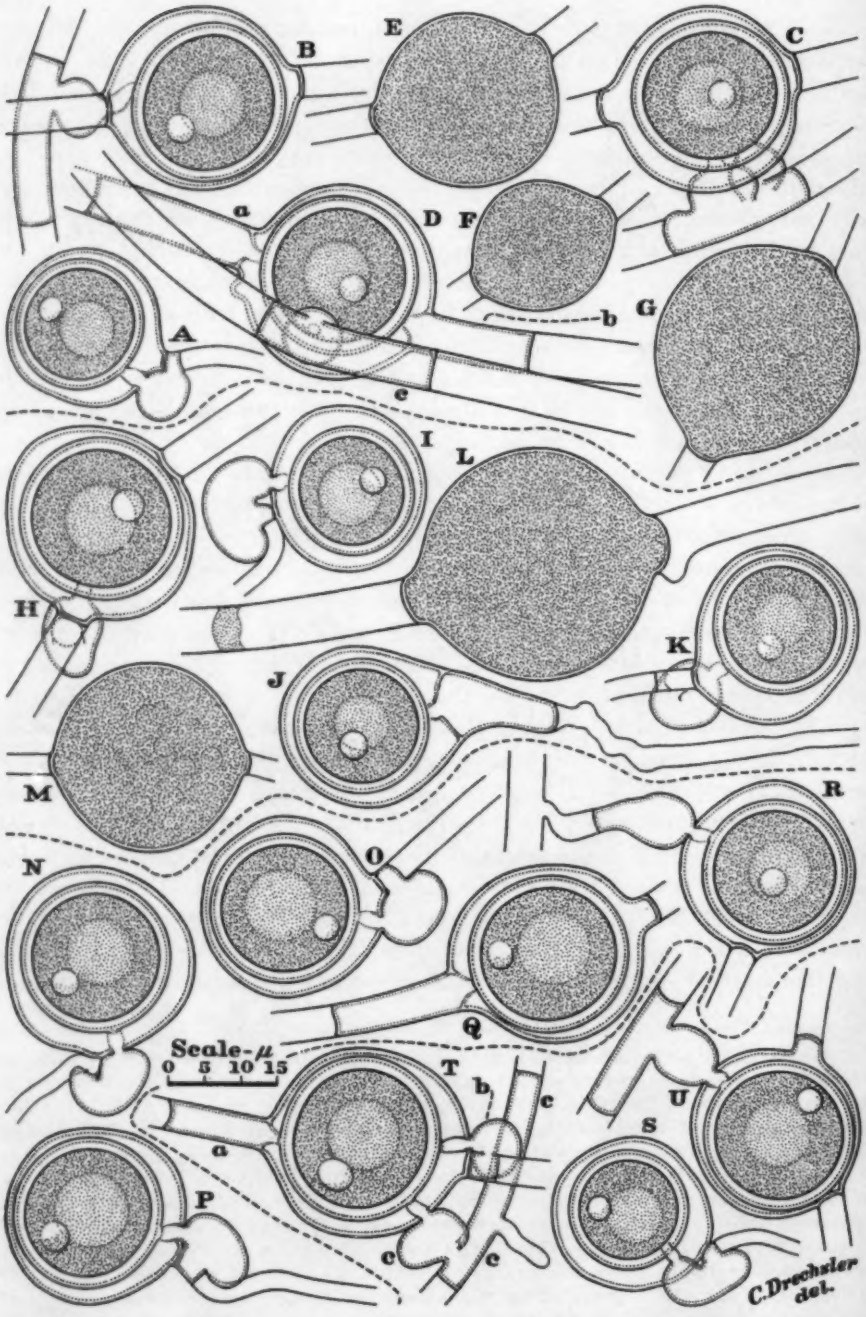


FIG. 6. *Pythium ultimum*, drawn to a uniform magnification from maizemeal-agar plate cultures, with the aid of a camera lucida; ×1000 throughout. Explanation of all parts and sources of all cultures given in text.

little change in their internal organization, and show correspondingly little increase in their capacity for prompt germination. However at temperatures ordinarily prevailing in laboratories, the changes of after-ripening become clearly noticeable in scattered oospores within about 25 or 35 days, and after 90 days by far the greater number of oospores will have lost their durable appearance and their inert behavior.

In the earlier stages of after-ripening the oospore of *Pythium ultimum* often contains 2, 3, or 4 refringent bodies (fig. 3, A; fig. 5, A) which sometimes are noticeably smaller than the single refringent body present at maturity. As their size and their luster diminish the plural refringent bodies are gradually lost to view in the protoplasmic mass surrounding them. Meanwhile the protoplasmic mass has gained in volume not only by resorbing in large part the thick yellowish inner layer of the oospore wall, but also by intermixing and merging with the material in the reserve globule (fig. 3, B; fig. 5, B). Consequently the after-ripened oospore is a rather thin-walled globose body filled with densely granular protoplasm in which about a dozen subspherical vacuoles, mostly 2 to 3.5 μ wide, are indistinctly visible. In its shape, as also in the character of its contents, it closely resembles conidia of mycelial origin (fig. 4, L, b; fig. 6, E–G, L, M) though its endogenous character is manifest in the presence of the normally persisting oogonial envelope. With respect to size, oospores, whether in a dormant or in an after-ripened condition, are generally somewhat less widely variable than conidia of mycelial origin. In most cultures they fail to attain the largest dimensions observable among asexual conidia.

When placed in fresh water the after-ripened oospore puts forth a broad protuberance which on reaching the oogonial envelope (fig. 3, C; fig. 5, C) soon pushes its way through that membrane to elongate externally (fig. 3, D, t; fig. 5, D, a: t). At temperatures near 10° C. the elongating germ tube frequently forms a hyaline cap of dehiscense (fig. 5, E, t) on reaching a length of 5 to 40 μ, though occasionally a germ hypha as much as 100 μ long is found apically modified for discharge (fig. 3, E, t). The protoplasmic contents migrate through the germ hypha (fig. 3, F, t. fig. 5, F, t; G, t) into a vesicle (fig. 3, F, v. fig. 5, F, v; G, v) and are there fashioned into laterally biciliate motile zoospores in the manner characteristic of the genus. After the swarmers have escaped from the evanescent vesicle, the empty evacuation tube (fig. 3, G, a–s: t; u: t. fig. 5, H–U: t) is found terminating abruptly at its open mouth, usually without any indication of being reflexed. Frequently the reduced wall of the oospore remains undivided throughout and may be shown advantageously as a double-contoured envelope slightly thicker than the oogonial membrane loosely surrounding it (fig. 5, H–U). Yet with respect to structure the reduced oospore wall would seem represented somewhat better as a triple-contoured envelope (fig. 3,

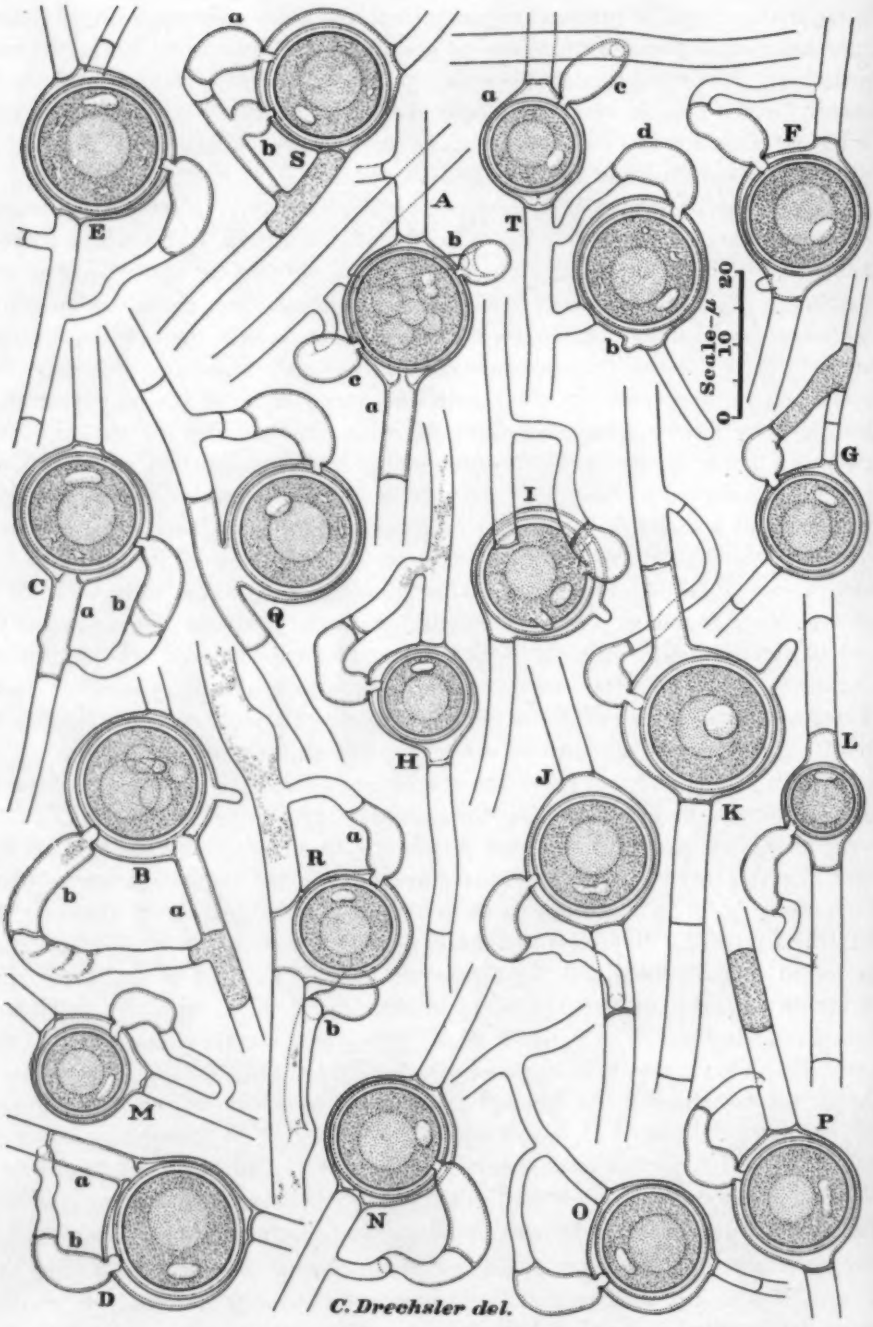


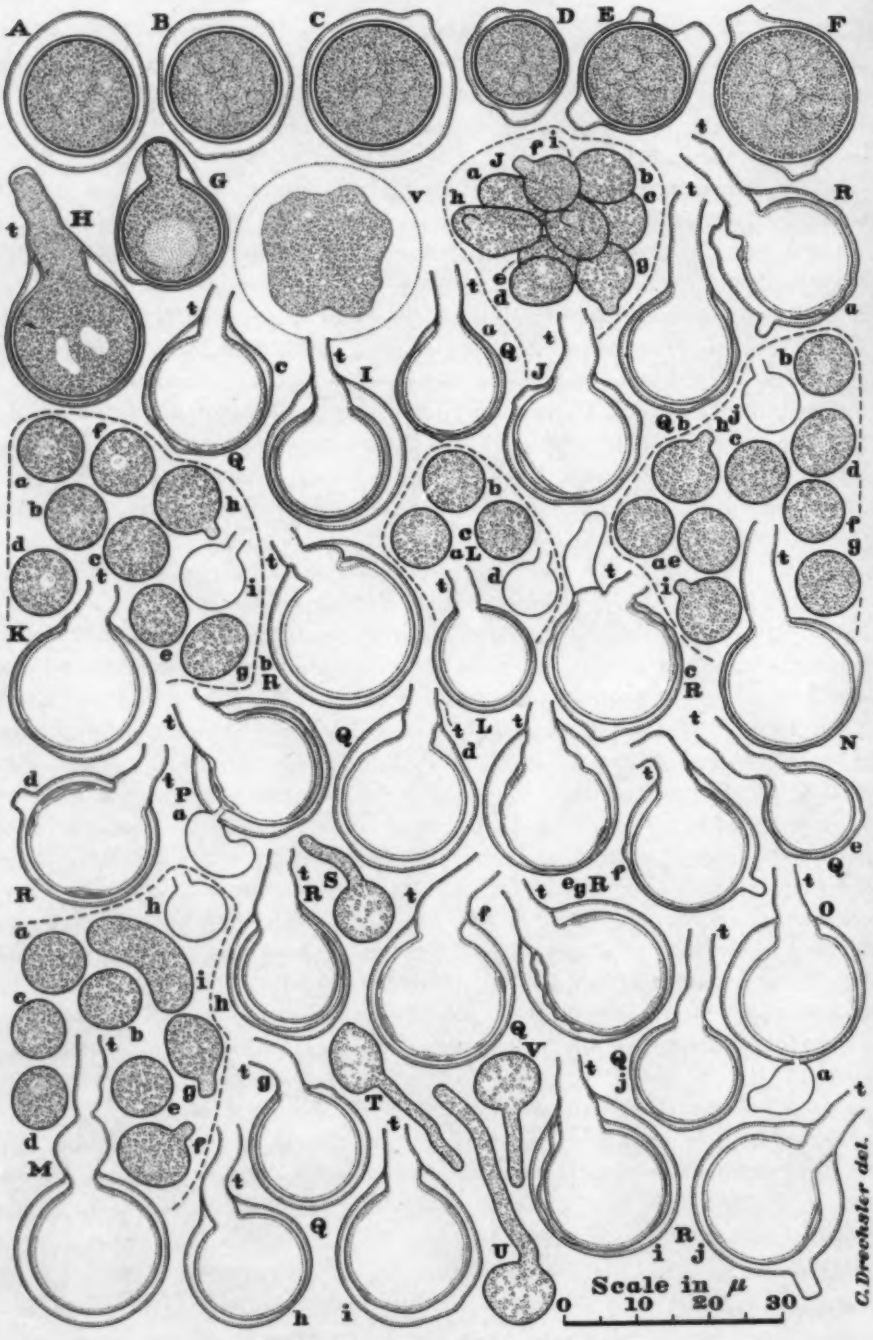
FIG. 7. Sexual reproductive apparatus of *Pythium debaryanum* drawn from maize-meal-agar plate cultures at a uniform magnification with the aid of a camera lucida; ×1000 throughout. Explanation of all parts given in text.

G, a–s, u) in which a thin colorless outer layer is distinguished from a thin, slightly yellowish, inner layer. Near the base of the evacuation tube the outer layer is sometimes found locally separated from the inner one (fig. 3, D; G, b, d, f, h, i, k, m–q, s, u) apparently as the result of tensions earlier exerted by the growing tube.

After-ripened oospores of approximately average size commonly yield 8, 9, or 10 motile zoospores (fig. 5, G), while those of greater or smaller volume give rise to swarmers in correspondingly larger or smaller numbers. Following a variable period of motility the zoospores normally round up into globose cysts mostly 8 to 10 μ, rarely up to 13 μ, in diameter (fig. 3, H; fig. 5, V, a–e). Some time later they usually germinate by putting forth a vegetative germ hypha (fig. 3, I, J; fig. 5, W, a, b), but occasionally where a temperature near 10° C. is maintained they will form a papilla of dehiscence (fig. 5, X, a, b) and discharge their protoplast to develop externally into a secondary swimmer. Each instance of such repetitional development leaves behind an empty subspherical cyst envelope that bears an evacuation tube open at its tip (fig. 5, Y, a, b).

As a rule when the germ hypha from an after-ripened oospore of *Pythium ultimum* has reached a length well in excess of 100 μ (fig. 1, A; fig. 5, Z) it is little likely to serve as an evacuation tube, but will almost certainly continue growth, whether under cold or under warm conditions, as a vegetative filament. In pure water such a germ hypha will often attain a length of 2 or 3 millimeters and may then, after some little branching, give rise to a conidium or in occasional instances to 2 or 3 conidia. The globose asexual reproductive bodies thus formed, either in intercalary (fig. 1, E, a–y) or in terminal positions (fig. 1, E, z), commonly measure 7.5 to 20 μ in transverse diameter. They are, of course, rather markedly smaller than the general run of ordinary conidia developed on well nourished mycelium in vigorous cultures. If the water in which they have been newly formed is replaced at intervals and if they are kept at a temperature near 10° C., a substantial proportion of them (fig. 1, F–N) will develop as zoosporangia by putting forth an evacuation tube (fig. 1, F–N:t) and then discharging their contents into a vesicle to be fashioned into motile zoospores.

In *Pythium debaryanum* production of zoospores is a commonplace phase of development and might, indeed, be nearly as familiar among students of plant diseases as Hesse's binomial, if only during winter our laboratory buildings were not heated so inexorably for tropical comfort. At the bracing temperatures between 16° and 18° C., which can sometimes be maintained in individual rooms by shutting off all radiators and closing all inside doors, ordinary conidia of the fungus will usually give rise to zoospores in ample abundance within a few hours after they have been placed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in a shallow layer of water, directly following their removal from maize-meal-agar cultures 10 to 20 days old. In an agreeably cool laboratory, zoospore production will often intrude spontaneously. Thus, in my experience, when thin slabs excised from agar cultures were examined under the microscope in sparingly moistened covered preparations, numerous conidia around the margin would frequently begin germinating within 30 minutes and in about 2 hours would be liberating active zoospores. More prolific zoospore development may be obtained through shallow irrigation of slabs excised from young Lima-bean-agar plate cultures.

The sexual reproductive apparatus of *Pythium debaryanum*, when considered collectively, is not difficult to distinguish from that of *P. ultimum*. In monoclinous units adjacent antheridia of cylindrical shape (fig. 7, A–D: a) are usually infrequent, and often are to be discovered only after some search. Most commonly antheridia of monoclinous origin are borne terminally on a branch arising at a distance from the oogonium about equal to the diameter of that organ (fig. 7, B–D: b; E–Q; R, a, b; S, a; T, d). On the whole the hyphal connection between the apposed sex organs would seem to correspond well to that shown in the relevant figures given by Hesse (1874, Tafel II, figs. 13, 14). Occasionally a male branch bearing a terminal antheridium may supply also an intercalary antheridium (fig. 7, S, b) provided with a protuberant part in contact with the oogonium. In dielinous reproductive apparatus the antheridium may be sessile (fig. 7, T, c), or may be borne terminally on a branch (fig. 7, A, b, c). As antheridial branches are conspicuously longer and more circuitous on moist agar media than on drier substrata, sexual apparatus produced on irrigated material appropriate for study of zoospore production often has a characteristically rangier appearance than the reproductive units illustrated herein (fig. 7, A–T).

FIG. 8. Germination of oospores from 90-day-old maizemeal-agar plate cultures of *Pythium debaryanum;* all parts drawn to a uniform magnification with the aid of a camera lucida; × 1000 throughout. A–F, Fully after-ripened oospores. G, Oospore in early stage of germination. H, Oospore with short germ tube, t, surmounted by cap of dehiscense. I, Empty envelopes of oogonium, oospore, and evacuation tube, t; v, vesicle containing uncleaved protoplasmic mass. J, Empty envelopes of oogonium, oospore, and evacuation tube, t, together with cluster of nine encysted zoospores, a–i. K–N, Empty membranous envelopes of oogonia and oospores, together with the concomitant encysted zoospores lying around or near the open tip of the evacuation tube, t, in numbers of nine (a–i), four (a–d), nine (a–i), and ten (a–j), respectively. O, Membranes left after germination of oospore by development of zoospores: a, empty antheridium; t, open evacuation tube; the oospore envelope here shows no separation of layers. P, Membranes like those in O, but oospore envelope here showing extensive separation into two layers. Q, Empty membranes of sexual reproductive units, a–j, including envelopes of oogonium, oospore, and evacuation tube, t, left after germination of oospore by production of zoospores; the oospore envelope not extensively separated into two layers. R, Empty membranes of sexual reproductive units, a–j, like those in Q, but oospore envelopes here somewhat more markedly or more extensively separated into two layers. S–V, Encysted zoospores, each germinating by production of a germ tube.

After fertilization is accomplished, development within the oogonium proceeds in *Pythium debaryanum* much as in *P. ultimum*. In the later stages of maturation an oospore may show several reserve globules (fig. 7, A, B). Completely mature oospores reveal the unitary internal organization most usual among members of the genus—a single central reserve globule being surrounded by a densely granular parietal layer within which is imbedded a single refringent body (fig. 7, C–S; T, a, b). The refringent body would seem generally somewhat more strongly flattened in *P. debaryanum* than in *P. ultimum*. The yellowish inner layer of the oospore wall is markedly thinner—commonly by about .4 or .5 μ—in the former species than in the latter. Indeed all associated membranous parts—the oogonial wall as well as the envelope of the antheridium and its supporting branch—appear generally thinner in *P. debaryanum*, are more often discernible only with difficulty, and are wont to vanish from sight earlier than in *P. ultimum*. Contrary to expectations that might be suggested by their less formidable incasement, the oospores of *P. debaryanum* are usually a little slower to show the internal changes which accompany after-ripening. On being stored for 90 days at ordinary room temperatures, maizemeal-agar plate cultures of *P. debaryanum* will often show approximately one-third of the oospores in a fully after-ripened condition, whereas in similar cultures of *P. ultimum* more than three-fourths will be ready for germination.

In *Pythium debaryanum* as in *P. ultimum* oospores capable of prompt germination (fig. 8, A–F) closely resemble conidia of mycelial origin—the wall being markedly reduced in thickness through resorption on its inner side, and the protoplasmic mass appearing of relatively uniform granular texture except for about a dozen globular vacuoles indistinctly visible in the central region. When some fresh water is supplied the oospore forms a protuberance that soon pushes against the oogonial envelope (fig. 8, G) and breaks through that barrier to elongate externally as a germ tube. Under warm conditions, as for example, at 28° C., a mycelium is regularly produced. At lower temperatures—I have used mainly temperatures near 10° and 17° C.—the germ tube likewise often keeps on growing vegetatively, but often, again, it stops growing when it has reached a length between 5 and 15 μ (occasionally when it has reached a length of 20 μ) and becomes modified as an evacuation tube (fig. 8, H, t) by forming a hyaline cap of dehiscense. The protoplasmic materials migrate through the tube (fig. 8, I, t) to collect within the vesicle (fig. 8, I, v) formed by inflation of the hyaline cap, and there are fashioned into laterally biciliate zoospores in the manner usual for the genus. In instances where from localized scarcity of water the zoospores are constrained to encyst in a cluster (fig. 8, J, a–i) or in a looser group (fig. 8, K, a–i; L, a–d; M, a–i; N, a–j) near the empty membranous envelopes, it is evident that oospores of average dimensions commonly yield about 9 or 10 swarmers, while others give rise to greater or

lesser numbers commensurate with their size. The empty membranous parts to which the antheridial envelope (fig. 8, O, a; P, a) is occasionally found attached sometimes shows the oospore wall with rather little or no separation into 2 layers (fig. 8, K–O; Q, a–j), but sometimes, again, fairly extensive separation (fig. 8, I; J; P; R, a–j) may be observed. The empty evacuation tube (fig. 8, I–P: t; Q, a–j: t; a–j: t) terminates abruptly without being widened or reflexed at the mouth, much as in *P. ultimum*, though generally it is shorter than in that species. The zoospores obtained through germination of oospores are indistinguishable, both in their motile and in their encysted condition, from those produced from sporangia of mycelial origin. After encystment they usually germinate by putting forth a vegetative germ hypha (fig. 8, S–V), yet at suitably low temperatures they sometimes form a papilla of dehiscence (fig. 8, J, f–i; K, h; M, f, g; N, h, i) and individually discharge their contents to be converted externally into a secondary motile zoospore. Where repetitional development has taken place, the empty cyst wall (fig. 8, K, i; L, d: M, h; N, j) bears an evacuation tube commonly 1.5 to 2.5 μ long and approximately 2 μ wide.

That after-ripened oospores of *Pythium debaryanum* will readily yield zoospores on germination is not surprising since the ordinary conidia of this fungus can usually be made to function as zoosporangia, whether they were nourished on artificial media, on mature vegetable tissues, or on seedlings of cultivated plants. In *P. ultimum*, however, production of zoospores from after-ripened oospores finds little analogous parallelism in the germinative behavior of the ordinary asexual conidia, though in a morphological sense these are hardly to be distinguished from the generally smaller conidia of germinative origin that so frequently develop as zoosporangia. Superior capabilities for zoospore formation have earlier been noted (Drechsler 1946b) in the after-ripened parthenospores of my *P. anandrum*, yet in that species zoospore development from ordinary asexual conidia is a well ascertained phase of reproduction, and can usually be induced with some patient effort. As has been mentioned previously (Drechsler 1946a), zoospore development in *P. ultimum* would seem adapted more especially for bringing about infection of rootlets in the deeper levels of the soil during the early cool part of the growing season—a frequent type of infection well exemplified in the sweetpotato rootlet rot from which the fungus shown in figures 4 and 5 was originally isolated.

SUMMARY

1. The features distinguishing *Pythium ultimum* and *P. debaryanum* in the formative and mature stages of sexual reproduction are reviewed and illustrated.

2. Oospores of both species become capable of germination after a resting period during which they acquire the structural characters of conidia.

3. At temperatures near 10° C. after-ripened oospores of *P. ultimum* will often germinate by producing zoospores.

4. Conidia formed on germ hyphae extended from after-ripened oospores of *P. ultimum* will likewise frequently develop as zoosporangia.

5. After-ripened oospores of *P. debaryanum* will readily give rise to zoospores at 10° C. as well as at temperatures near 17° C., their germinative behavior not differing noticeably from that of the ordinary conidia produced asexually by the fungus.

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DIFFERENTIAL REACTIVITY IN SIX SPECIES OF TRILLIUM

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Exposure to cold treatment for a sufficient length of time produces regions of differential reactivity along the length of metaphase and anaphase chromosomes of *Trillium* (Darlington and LaCour 1940). These differential segments usually appear to be understained and of reduced diameter. According to Darlington and LaCour (1940) each chromosome has a characteristic pattern of differential reactivity, although the size of the segment may be subject to some variation.

The length of cold treated chromosomes has also received attention. Darlington and LaCour (1940) report that the chromosomes "remain their usual length" after cold treatment. Wilson and Boothroyd (1944) observed "greater than normal mitotic contraction" of chromosomes of *Trillium* after exposure to low temperatures. Bailey (1949) found that the chromosomes of *T. erectum* L. measured 93.5% of their normal total length after cold treatment.

Salord (1949) with respect to contraction of the chromosomes of *T. grandiflorum* (Michx.) Salisb. after exposure to cold treatment states that, "the contractions which Wilson and Boothroyd (1944) observed in the non differentiated regions, do not exist in individuals observed in this species". In *T. luteum* (Muhl.) Harbison he states that, "at 3°, 2°, and 0° C. the behavior of the chromosomes is the same as the surrounding temperature of plus or minus 20° C." Speaking of *T. sessile* L. Salord (1949) says that, "this species has made it very obvious that the contraction not only varies from species to species but also considering in each species individuals of identical size, the interspecific difference among them is less than that observed in the same species among individuals of different sizes (cf. Resende, Salord, and Leite-Rio. 1949)".

Darlington and LaCour (1938) suggest that differential reactivity may be used as a genetic and taxonomic indicator, a criterion of variation between species. Studies by Wilson and Boothroyd (1941 and 1944) and Bailey (1949) show that the pattern of differential segments produced as a result of cold treatment is not the same in *T. erectum* L. collected in Canada and *T. erectum* L. collected in Tennessee. This indicates that the position of differential segments is not constant and specific for a given species. Perhaps there are certain segments which are constant and specific as to position for a given species, but this remains to be seen. It was the primary purpose of this study to determine whether the pattern of differential segments is the same or different in six of the sessile species of *Trillium* collected in Alabama.

Materials and methods. Six different species of *Trillium* were used in this study. Rhizomes were collected from various localities and fresh growing root tips were used as a source of material. *Trillium decumbens* Harbison was collected from Blount County, Alabama, *Trillium sessile* L. from Shelby County, Alabama. *Trillium lancifolium* Raf. from Tuscalloosa County, Alabama and *Trillium recurvatum* Beck and *Trillium stamineum* Harbison from Cullman County, Alabama. Rhizomes of *Trillium luteum* (Muhl.) Harbison were furnished by Dr. Joe A. Chapman of Carson-Newman College, Jefferson City, Tennessee. Cold treatment was provided with a commercial electric refrigerator which maintained a fairly constant temperature at 3° C. The cold-treated root tips were secured from rhizomes which had been potted in peat moss before being transferred to the refrigerator. All tips used in this study were exposed to cold for 96 hours.

All material for study was prepared using the Feulgen technique together with a squash method (Woodard 1948). All measurements were made on metaphase chromosomes using an ocular micrometer.

Observations and discussion. *Trillium decumbens* Harbison. The regularly recurring pattern of differential segments produced after exposure to 3° C. for 96 hours in *T. decumbens* Harbison is shown in figure 1. Chromosomes A, B, and C show regions of differential reactivity whereas chromosomes D and E fail to show any such regions.

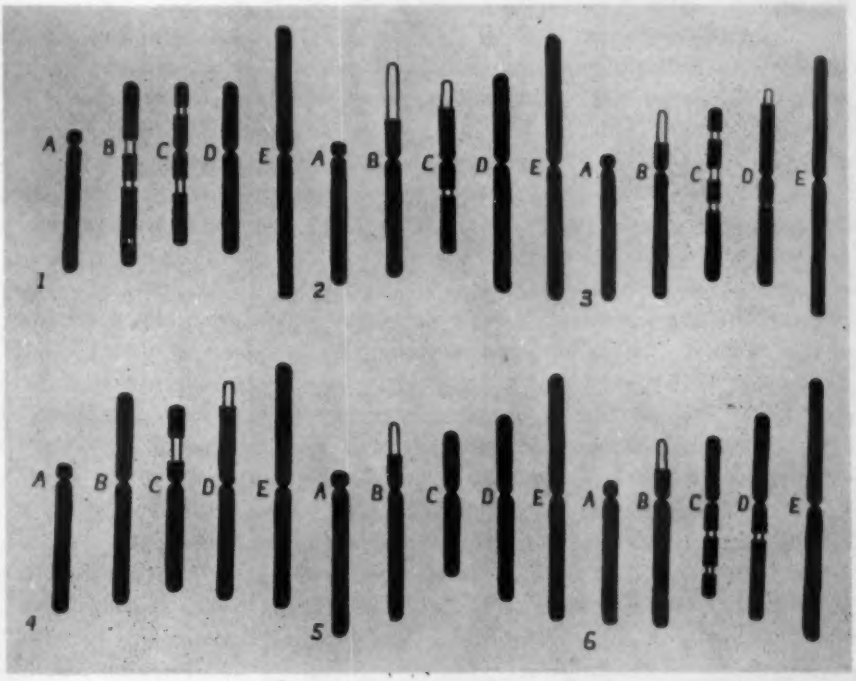
Chromosome A failed to show any differential segments in about 20 per cent of those studied. In the 80 per cent which did show regions of differential reactivity the segment appeared as a sub-median, understained line reaching across the diameter of the chromosome. The portion of the chromosome arm distal to the differential segment is 10.9 microns in length whereas the proximal portion is 3.3 microns. This makes a total length of 14.2 microns for the long arm of chromosome A. The short arm measures 1.6 microns, making a total length of 15.8 microns for chromosome A.

Chromosome B shows two regions of differential reactivity as a result of cold treatment. One of these differential segments is the region of the primary constriction which is 1.4 microns long. The other differentially reactive segment of chromosome B is a sub-median one located in the long arm. It is 0.8 micron long. The distal portion of the chromosome arm is 8.8 microns whereas the proximal portion is 3.0 microns long. This makes a total length of 12.6 microns for the long arm of chromosome B. The short arm of chromosome B measures 6.6 microns making a total length of 20.6 microns for chromosome B.

Chromosome C shows two regions of differential reactivity, one in each arm. The differential segment in the short arm is a sub-median one and is 0.8 micron long. The distal portion of the short arm is 2.5 microns long whereas the proximal portion measures 4.0 microns in length. This gives a

length of 7.3 microns for the short arm. The differential segment in the long arm of chromosome C is a sub-median one, 1.6 microns long. The proximal portion of this arm is 3.3 microns whereas the distal portion measures 5.9 microns. This gives a total length of 10.8 for the long arm and a total length of 18.1 microns for chromosome C.

Chromosomes D and E show no regions of differential reactivity after cold treatment for 96 hours. Chromosome D shows a total length of 19.1 microns and chromosome E a length of 30.6 microns after exposure to cold.



FIGS. 1–6. Diagrammatic analysis of chromosome morphology of several species of *Trillium* after cold treatment. FIG. 1. *T. decumbens* Harbison. FIG. 2. *T. lancifolium* Raf. FIG. 3. *T. luteum* (Muhl.) Harbison. FIG. 4. *T. stamineum* Harbison. FIG. 5. *T. recurvatum* Beck. FIG. 6. *T. sessile* L. All figures are drawn to scale at an approximate magnification of ×1240 after reduction.

The total length of the chromosome set (2n) after cold treatment is 208.4 microns. Before cold treatment (Bailey 1951) the total length was 166.6 microns. This gives an increase of 41.8 microns as a result of cold treatment. The arm-length ratios are approximately the same before and after exposure to cold.

Trillium lancifolium Raf. Two chromosomes of *T. lancifolium* Raf. regularly show regions of reduced diameter and staining capacity as a result of cold treatment (fig. 2). Chromosome B shows one region of differential

TABLE 1. *Comparative data on chromosome morphology of some species of Trillium after cold treatment*

Material	Chromosome A			Chromosome B			Chromosome C			Chromosome D			Chromosome E			Total
	L.A.	S.A.	T.L.	L.A.	S.A.	T.L.	L.A.	S.A.	T.L.	L.A.	S.A.	T.L.	L.A.	S.A.	T.L.	
1. *T. decumbens* Harbison	14.2	1.6	15.8	12.6	6.6	20.6	10.8	7.3	18.1	11.2	7.9	19.1	16.0	14.6	30.6	208.4
2. *T. lancifolium* Raf.	14.5	1.6	16.1	13.4	10.4	23.8	10.4	8.8	19.2	14.3	9.8	24.1	14.9	14.6	29.5	225.4
3. *T. luteum* (Muhl.) Harbison	14.7	1.6	16.3	14.2	7.0	21.2	11.7	6.4	19.3	12.4	9.9	22.3	15.2	13.9	29.1	216.4
4. *T. stamineum* Harbison	14.1	1.6	15.7	13.3	9.4	22.7	11.4	9.5	20.9	12.4	10.9	23.3	13.2	13.2	26.4	218.0
5. *T. recurvatum* Beck	16.1	1.6	17.7	14.1	7.2	21.3	9.4	6.3	15.7	11.6	8.9	19.9	13.5	13.1	26.6	204.4
6. *T. sessile* L.	13.8	1.6	15.4	14.0	6.4	20.4	10.6	6.6	17.2	12.9	9.3	22.2	14.9	13.6	28.5	207.4

L.A.—Long arm; S.A.—Short arm; T.L.—Total length.

reactivity in the short arm after exposure to 3° C. for 96 hours. This is a terminal differential segment and is 6.1 microns long. The portion of the chromosome arm proximal to this segment measures 4.3 microns, making a total length of 10.4 microns for the short arm. The long arm of chromosome B measures 13.4 microns. This gives a total length of 23.8 microns for chromosome B.

Chromosome C shows two regions of differential reactivity, one in each arm. The differential segment in the short arm is a terminal one and measures 2.7 microns. That portion of the short arm proximal to this segment is 6.1 microns. The differential segment in the long arm is a sub-median one and is 0.8 micron in length. The proximal portion of the long arm measures 3.3 microns whereas the distal portion measures 6.3 microns. This gives a total length of 19.2 microns for chromosome C.

Chromosomes A, D, and E fail to show any differentially reactive regions after cold treatment. Chromosome A shows a total length of 16.1 microns, chromosome D 24.1 microns, and chromosome E 29.5 microns after exposure to cold.

The total length of the diploid chromosome set after cold treatment was 225.4 microns whereas before treatment the total length was 192.9 microns (Bailey 1951). Arm-length ratios are approximately the same before and after cold treatment.

Trillium luteum (Muhl.) Harbison. Chromosomes A and E of *T. luteum* (Muhl.) Harbison (fig. 3) fail to show any differential segments after exposure to cold. Chromosome A shows a total length of 16.3 microns whereas chromosome E has a total length of 29.1 microns after treatment.

Chromosome B shows one differential segment after cold treatment. This segment is a terminal one located in the short arm and measures 3.7 microns. The proximal portion of the short arm is 3.3 microns long. The long arm measures 14.2 microns, making a total length of 21.2 microns for chromosome B.

Chromosome C shows three regions of differential reactivity. The primary constriction is one differential region and is 1.2 microns in length. A sub-median differential segment is found in each arm of chromosome C. The differential segment in the short arm is 1.0 micron long. The length of the chromosome arm distal to this segment is 2.3 microns whereas the proximal portion is 3.1 microns in length. This gives a length of 6.4 microns for the short arm. The differential segment located in the long arm is 0.9 micron in length. The distal portion of the chromosome arm is 7.9 microns and the proximal portion is 2.9 microns. This gives a length of 11.7 microns for the long arm and a total length of 19.3 microns for chromosome C.

Chromosome D regularly shows a terminal differential segment in the short arm. This segment measures 1.6 microns. The proximal portion of this chromosome arm is 8.3 microns. A sub-median differential segment is found

in the long arm. This segment is very short and appears only as an understained line across the diameter of the chromosome arm. The proximal portion of this chromosome arm measures 3.3 microns and the distal portion 9.1 microns. This gives a total length of 22.3 microns for chromosome D.

The total length of the normal diploid chromosome set was 193.6 microns (Bailey 1951). After exposure to 3° C. for 96 hours the total length is 216.4 microns. Arm-length ratios are approximately the same before and after treatment.

Trillium stamineum Harbison. Chromosomes C and D of *T. stamineum* Harbison (fig. 4) regularly show regions of differential reactivity. The differential segment of chromosome C is a sub-median one in the short arm (fig. 4). This segment is 2.9 microns long. The proximal portion of this chromosome arm is 3.3 microns in length whereas the distal portion is also 3.3 microns long. The long arm of chromosome C is 11.4 microns in length, making a total length of 20.9 microns for chromosome C.

The differential segment of chromosome D (fig. 4) is a terminal one occurring in the short arm. This segment measures 2.6 microns and the proximal portion of this chromosome arm is 8.3 microns in length. The long arm measures 12.4 microns, giving a total length of 23.3 microns for chromosome D.

Chromosomes A, B, and E fail to show regions of differential reactivity after cold treatment. Chromosome A measure 15.7 microns, chromosome B 22.7 microns, and chromosome E 26.4 microns.

Before cold treatment the normal chromosome set (2n) of *T. stamineum* Harbison measured 179.9 microns. After cold treatment the total length was 218.0 microns. Arm-length ratios are approximately the same before and after cold treatment, but somewhat larger after treatment.

Trillium recurvatum Beck. Only one differentially reactive segment occurs in the chromosome complement of *T. recurvatum* Beck (fig. 5). This segment is a terminal one found in the short arm of chromosome B and measures 3.3 microns. The proximal portion of this chromosome arm is 3.9 microns in length. The long arm of chromosome B is 14.1 microns long. This gives a total length of 21.3 microns for chromosome B.

Chromosomes A, C, D, and E show no differential segments after exposure to cold. After cold treatment chromosome A measures 17.7 microns, chromosome C 15.7 microns, chromosome D 19.9 microns, and chromosome E 26.6 microns.

The total length of the diploid chromosome set for *T. recurvatum* Beck before cold treatment measured 180.1 microns whereas after treatment the total length measured 204.4 microns. No significant variations occur in the arm-length ratios before and after cold treatment.

Trillium sessile L. Chromosomes B, C, and D in *T. sessile* L. regularly

show regions of differential reactivity as a result of cold treatment (fig. 6). The differential segment found in chromosome B is a terminal one located in the short arm. This segment measures 3.2 microns in length whereas the proximal portion of this arm is 3.2 microns long. The long arm of chromosome B is 14.0 microns in length, making a total length of 20.4 for chromosome B.

Chromosome C shows two differential segments in its long arm. Both differential segments measure 0.8 micron in length. The proximal portion of this arm is 3.2 microns long, the distal portion 2.6 microns, and the unaffected portion between the differential segments measures 3.2 microns. The short arm is 6.6 microns in length, giving a total length of 17.2 microns for chromosome C.

Chromosome D shows one sub-median differential segment located in its long arm. This segment is 0.8 micron in length. The proximal portion of this chromosome arm is 3.2 microns long whereas the distal portion measures 8.9 microns. The long arm is 9.3 microns long, making a total length of 22.2 microns for chromosome D.

Chromosomes A and E fail to show differential reactivity as a result of cold treatment. After treatment chromosome A measures 15.4 microns and chromosome E shows a length of 28.5 microns.

Before cold treatment the normal chromosome set (2n) for *T. sessile* L. measured 177.9 microns (Bailey 1951). After exposure to cold the total length of the chromosome set measured 207.4 microns. Arm-length ratios show no significant variations before and after cold treatment.

Comparative data on the chromosome morphology of the six species of *Trillium* included in this study is summarized in Table 1. Table 1 shows the total length of the chromosome (2n) complement after cold treatment as well as the length of individual chromosomes and the length of the chromosome arms.

SUMMARY

1. The pattern of differential segments produced as a result of cold treatment for 96 hours is different in each of the six species included in this study.

2. The total length of the diploid chromosome set increases after cold treatment in each of the six species. The increase ranges from 22.8 microns in *T. luteum* (Muhl.) Harbison to 41.8 microns in *T. decumbens* Harbison.

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EFFECT OF VARIABLE VAPOR CONCENTRATIONS OF ETHEREAL OILS UPON TRANSPIRATION AND WATER ABSORPTION[1]

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It has been assumed that the ethereal oils may be a factor regulating the rate of transpiration. But a survey of the literature on the subject discloses that, except for some few meager experiments, no attempts have been made to verify this assumption.

At the middle of the last century (1862) the physicist Tyndall reported some experiments in which he passed air through cylinders of cardboard soaked in various essential plant oils, and then determined its perviousness to thermal radiation in each case. He came to the conclusion that a layer of air, saturated with the vapor of an ethereal oil is much less pervious to heat radiations than an equally thick layer of pure air. Detto (1903), showed that the statistics of the plants of Germany indicated the lack of an overbalance of aromatic plants in xerophytic formations of its flora. After a good deal of argument he was led to believe that ethereal oils are better regarded as a successful means of protecting not only leaves secreting them but also the reproductive organs against animals. Dixon (1914) performed some preliminary experiments testing the effect of some essential plant oils upon transpiration. In one of his experiments, Dixon found that, if the rate of transpiration of a branch of *Syringa vulgaris* L. in a current of dry air, was denoted by 100, this rate was reduced to about 87 if the air current was allowed to pass over chopped leaves of *Artemisia Absinthium* L. Dixon was of the opinion that the presence of such a heat-absorbing layer of oil vapor in contact with the leaves secreting them would tend to raise their temperature. He believed that the oil vapors exerted a retarding action on evaporation from the mesophyll tissue of leaves by depressing the activity of the protoplasm.

Thus we see that, except for the few experiments of Dixon, it was not until the previous work of the author (Gamil 1939) that the subject of ethereal oils and their effect upon transpiration received any further attention. Since that work was not published, an account of it will be given here before dealing with the present investigation.

A study of the effect of several ethereal oils upon the transpiration rate of cut branches of *Eucalyptus rostrata* Schlecht. and *Alhagi maurorum* Medic., and whole plants of *Mentha piperita* L. and *Euphorbia Peplus* L.

[1] Thanks are due to Prof. H. Said, Head of the Physiology Department for advice and support.

showed that the application of relatively low vapor concentrations of ethereal oils depressed their rate of transpiration. These observations were in accord with the results obtained by Dixon. On the other hand, the application of appreciably high concentrations of such oil vapors brought about a significant promotion in the rate of transpiration of the same plants under similar conditions. It then appeared preferable to limit the investigation to testing the effect of only low concentrations of the vapor which were believed to be more or less equal to those expected in nature.

The discovery that a low concentration of an ethereal oil vapor caused a decrease in the rate of water-loss from a transpiring plant immediately raised the question of the cause of that decrease. The two possibilities that presented themselves in that connection were: 1—Their effect was upon the diffusion of water vapor from the stomatal pores and from the surface of the leaf. 2—Their effect was upon the diathermancy of air to radiant energy and consequently upon the leaf temperature of plants.

Experiments were performed to test the influence of ethereal oils upon the diffusion of water vapor molecules from the surface of a moist filter paper. It was found that the rate of evaporation was always diminished immediately after the addition of an oil vapor. It was assumed that the vapors of these ethereal oils, forming a shell in the immediate vicinity of the moist surface, might be regarded as a physical boundary, which would obstruct the diffusion of the water molecules. The fact that transpiration is essentially a process of evaporation led the author to expect that ethereal oils might influence the process in much the same way as they influence evaporation.

In support of the second possibility, a simple experiment showed that air saturated with an oil vapor transmitted less thermal radiation than oil-free air. A glass tube, 50 cm. long and 5 cm. in diameter, was fitted with cork stoppers at the ends. Each cork had a central circular aperture, 2 cm. in diameter, which was perfectly closed by a cover-slip cemented with Canada Balsam on the inner side of the cork. Through a hole in the cork there passed a delivery tube by means of which the tube could be charged with the required atmosphere. The tube was placed between a source of heat at one end and a thermopile at the other end. The tube was first filled with ordinary air and the deflection of a sensitive galvanometer spot noted. The tube was then charged with oil-saturated air and the new deflection observed. In that way experiments showed that thermal radiations were transmitted less freely through air saturated with an oil vapor than through pure air.

Recognizing this fact, an attempt was made to show that the leaf of a plant in an oil-saturated atmosphere would be slightly cooler than the leaf of another plant under ordinary atmospheric conditions. Two glass tubes,

about 20 cm. long and 5 cm. in diameter and fitted at one end with cork stoppers similar to those described above, were supported horizontally and inclined to each other towards an electric lamp with a reflector behind. Facing the distal unstoppered end of each tube there was a leaf of a potted plant holding an iron-constantan differential thermocouple on its lower surface and receiving the rays emerging from the tube normal to its upper surface directly over the thermocouple. The measurements of the changes in leaf temperature, following changes in energy receipt, were made by the deflection of a sensitive high resistance mirror galvanometer connected directly to the copper leads of the differential thermocouple. Differences of temperature of 1/110° C. could easily be detected. In between the two tubes a diaphragm of cardboard was interposed so as to prevent as much as possible the diffusion of the oil vapor from one compartment to the other. In performing an experiment, both tubes were at first filled with common air and the galvanometer was brought to zero, indicating no temperature difference between the two leaves subjected to the experiment. Into one of the tubes oil-saturated air was then introduced and the observed deflection showed the leaf temperature of the treated one to be, from 0.5 to 1.0° C. lower than its oil-free control. The reverse effect was true of experiments in which a flask containing ice-shavings replaced the lamp. Theoretical considerations indicated that hand in hand with the fall of leaf temperature went a drop of the vapor pressure within the leaf, thus decreasing the vapor pressure difference, and correspondingly retarding transpiration.

The observed depression in the rate of water-loss in response to oil treatment, may not be ascribed solely to the two above mentioned factors, namely, the reduction of the diffusion of water vapor along the stomatal pores and the fall of leaf temperature, but it may also be due in part to some other factor or factors which will be revealed by further investigations.

After these experiments had been completed and before the present investigation was started, the author's attention was drawn to a paper by Audus and Cheetham (1940) on the significance of ethereal oils in regulating leaf temperatures and transpiration rates. These authors used cherry laurel treated with vapors of certain essential oils. The rate of water absorption by the treated shoots was taken as a direct measure of the transpiration rate. A dry air-current was allowed to flow through a tower containing cotton-wool soaked in the oil under test before passing through the chamber enclosing the plant material. In this way the applied vapor concentrations were of unknown values. The general conclusions of these authors were somewhat different from those given above. Exposure of shoots of cherry laurel to streams of air saturated with vapors of some essential plant oils failed to produce any measurable effect on either the transpira-

tion rate, leaf temperatures, or stomatal resistance. Nevertheless, in some of their experiments rosemary oil vapor seemed to effect a small decrease in the transpiration rate. These authors concluded that oil vapors might produce a reduction in the total energy incident on the leaf surface, but that the effect was overbalanced by an opposing effect arising from a depression of the transpiration rate. They attributed that depression to a toxic action of the vapors. It must be remembered that these authors did not use a control arrangement running side by side with experimental treatments. This uncontrolled method of experiment seems open to criticism, for unless untreated material is used for comparison false conclusions may be reached especially in cases where the effect due to treatment is small.

From the experimental procedure followed by Audus and Cheetham it is obvious that it was actually the rate of water-absorption rather than the rate of transpiration which failed to respond to oil treatments. These authors formulated their conclusions on the assumption that the transpiration rate, during the test period, necessarily followed the rate of water absorption. This is not likely, as it has already been stated that the application of ethereal oil vapors to a transpiring plant member did appreciably affect its rate of water loss. Further evidence will be given in the present paper.

After reviewing all the work done previously in this field, it seemed desirable to carry out some further experiments in which variable concentrations of different ethereal oils would be tested. Preliminary experiments were performed for testing the effect of relatively high vapor concentrations of such ethereal oils. Cut branches of a plant not naturally producing oils were first used in order to investigate the possible effects of oil vapors on its leaves, and also to avoid any possible complications which might arise from the added action of the oils secreted by the plant itself. For the sake of comparison, experiments were then conducted with branches of a plant naturally secreting an ethereal oil in its leaves and treated with either its own or some other essential oil. *Alhagi maurorum* Medic. and *Eucalyptus rostrate* Schlecht. were chosen for this study.

The experimental procedure was the one described previously. Two separate lots of young branches, of more or less equal weights, were used, one serving as a control. Branches were inserted, after taking the usual precautions to prevent the entrance of air in the xylem, into a test tube containing water, hanging from one arm of a sensitive balance. The plant material was enclosed in a large glass chamber through which a flow of dried air was circulated by means of an electric blower at a constant rate, sufficient to remove all the moisture.

At the outset of an experiment pure air was allowed to circulate and and the rate of transpiration was directly estimated by weighing the amount of moisture lost from the given branches at intervals of fifteen minutes.

After a period of time and when the vapor of the ethereal oil under investigation was to be admitted a bottle containing the oil was introduced into the air stream between the air drying materials and the chamber enclosing the plant material. In this way the air current was charged with the oil vapor before passing over the transpiring material. The vapor concentration could be changed at will. Determinations of water-loss per fifteen minutes were continued. After a further period of time the oil-container was removed and pure air was allowed to flow again through the chamber. A similar arrangement of the apparatus just described was used as a control. The control material was continually supplied with a current of pure, dry air of the same velocity as that circulating around the experimental material.

To ensure constant light conditions, the plant material was illuminated continually by three 100-Watt lamps, throughout the experiment, as natural daylight was variable. A mercury thermometer subdivided into 0.1 C. recorded air temperatures which used to fluctuate within $\pm 1^\circ$ C.

The results of the experiments are illustrated in figure 1 in which the ordinates are milligrams of water actually lost per fifteen minutes. It has been thought unnecessary to reduce these amounts to a uniform area or weight of leaf, for the main object was just to demonstrate the changes in the rate of water loss of the treated plants in response to oil treatment. The abscissae are intervals of fifteen minutes from the start of the experiment.

An examination of the figure demonstrates conclusively that relatively high vapor concentrations of ethereal oils passed over a transpiring plant to bring about an appreciable though gradual increase in the transpiration rate.

Experiment IV was intended to demonstrate the effects of relatively low and higher vapor concentrations of eucalyptus oil upon one and the same plant material. The application of a low vapor concentration resulted in a slight decrease of the transpiration rate (about 5% lower than that of its control). After a period of one hour, the vapor concentration in the circulating atmosphere was considerably increased. This resulted in a rapid and considerable increment in the rate of water-loss to much above the normal value (about 35% higher than that of its control). After a further period of 45 minutes, the oil vapor was completely cut off and the rate of transpiration declined rapidly to a low value. It is worthy to record that in all the preliminary experiments, relatively high vapor concentrations considerably and consistently caused the plant leaves to turn yellow and show signs of wilting at the end of experiment.

With regard to the depressive effect of relatively low and the augmentative effect of higher vapor concentrations of ethereal oils upon the rate of water loss from a transpiring plant, it is suggested that this may be due to changes in the permeability of the plant tissues under treatment, and

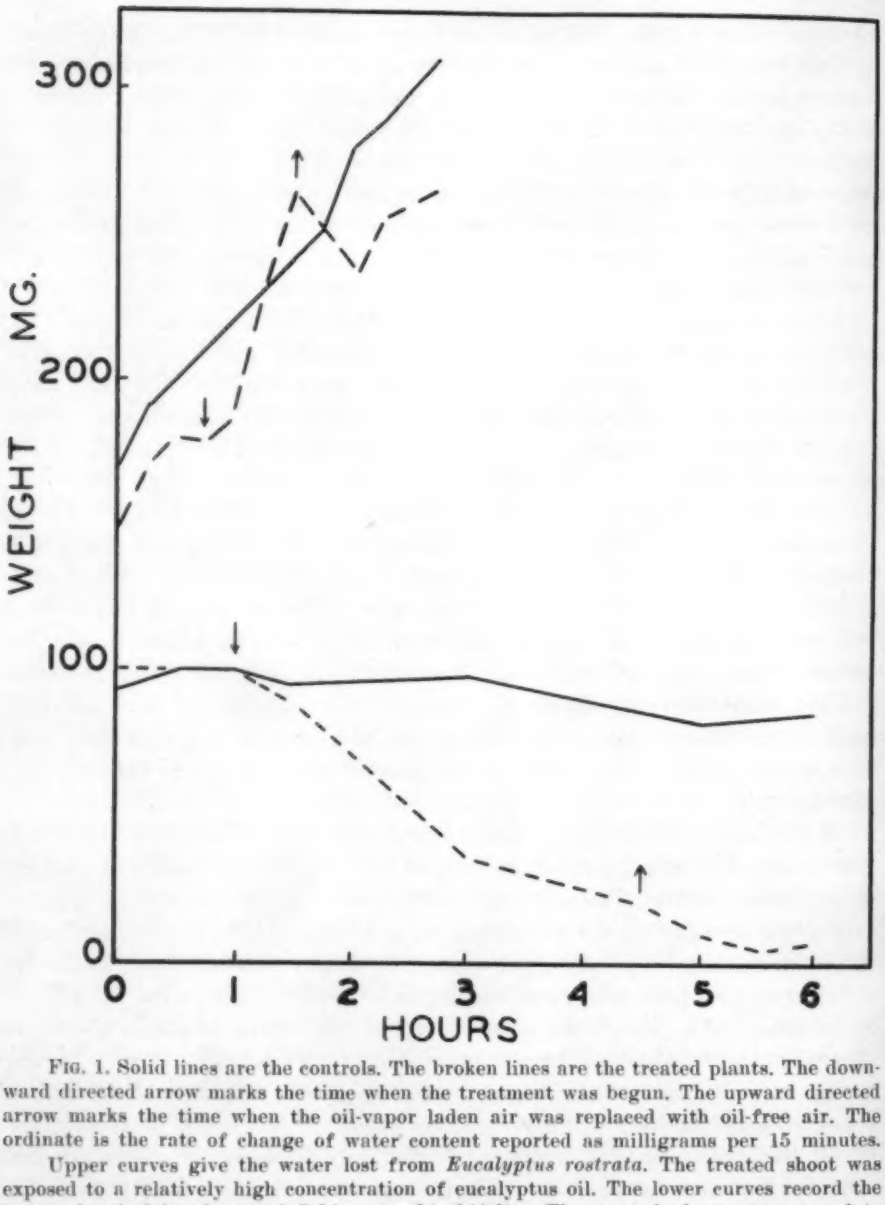

FIG. 1. Solid lines are the controls. The broken lines are the treated plants. The downward directed arrow marks the time when the treatment was begun. The upward directed arrow marks the time when the oil-vapor laden air was replaced with oil-free air. The ordinate is the rate of change of water content reported as milligrams per 15 minutes.

Upper curves give the water lost from *Eucalyptus rostrata*. The treated shoot was exposed to a relatively high concentration of eucalyptus oil. The lower curves record the water absorbed by shoots of *Schinus te. binthifolius*. The treated plant was exposed to eucalyptus oil of a concentration of 38.5 mg. per liter of air.

that there may be a relationship between the transpiratory values and changes of permeability. In this connection one is reminded of the action of anaesthetics in bringing about changes in the permeability of cell membranes.

Under the influence of an anaesthetic, such as chloroform, Lepeschkin (1906) showed that the exudation of water from the sporangiophore of *Pilobolus* can be diminished by a small dose of chloroform gradually applied, indicating a decrease of permeability, whereas a large dose increased the permeability. Later, numerous observations were made by Irving (1911) and Thoday (1913) on the effect of different doses of chloroform upon respiration and assimilation. Under the influence of this anaesthetic, some other effects upon leaves, including the exudation of drops of water on surface of leaves, have been recorded by these authors.

Accordingly an observation of the variable responses of a transpiring plant to different vapor concentrations of an ethereal oil receives a plausible explanation. The decreased water loss which followed the treatment with a relatively low or moderate vapor concentration is assumed to be, at least partly, due to a decrease of permeability, whereas a higher vapor concentration increases the permeability of treated tissues to water.

The effect of definite vapor concentrations of ethereal oils upon the water balance relationships of plants. In the above experiments the supply of oil vapor was not controlled and, as a consequence, the exact concentration in the atmosphere surrounding the transpiring plant at any time could not be known. It seemed, therefore, necessary to study the effect of ethereal oils upon the water balance relationships of plants under controlled conditions of oil treatments.

For the sake of comparison with the work of Audus and Cheetham (1940), who used the rate of water absorption as a measure of transpiration, the same procedure was followed. Two separate young branches of *Schinus terebinthifolius* Raddi. or of *Alhagi maurorum* were employed simultaneously, one serving as a control. Each weighed about five grams and possessed, as far as it was practicable, the four youngest leaves so that the samples were comparable with respect to the age factor. The cut end of the branch was inserted into a potometer which passed through a rubber-stopper fitted in the mouth of a bottle of about 750 ml. capacity serving as a chamber enclosing the plant material. The two chambers were immersed in a large thermostat, kept at a constant temperature of 30° C. throughout the course of an experiment. Each chamber was illuminated by a 300-Watt lamp placed at about 20 cm. from the chamber. Oil was introduced at will into one of the closed circuits before the air passed through the chamber. Air flow through both chambers was kept equal by means of gas-meters. The temperature of the air was maintained constant by passing the air current through a glass coil immersed in the thermostat before circulating through the chamber containing the plants. At the beginning of each experiment the air current was allowed to run for a preliminary one hour before any actual estimations were recorded. At the end of the period

of exposure to the vapor, the weight of oil evaporated was measured, the number of liters of air passed through the apparatus during that period was recorded by a gas-meter, and the exact concentration of the oil per liter of air current was calculated.

The results of three of these experiments are similar to the lower curves in figure 1.

From the experimental results it is clear that the effect of applying eucalyptus oil vapor, at relatively high concentrations, is to bring about a fall in the rate of water absorption. This fall is gradual at first, but steepens afterwards until a very low value is reached. In each case this is accompanied by visible deleterious effects such as change of color and obvious wilting. Comparing this behavior with what happens in nature, one has to bear in mind that essential plant oil concentrations produced by volatilization from leaves have no effect whatsoever on the healthiness of plant tissues. This means that the experimental eucalyptus oil concentrations are undoubtedly higher than could arise by evaporation of this oil from leaves in nature. Upon the removal of eucalyptus oil vapor in experiments VI and VII (fig. 1) the treated materials did not recover their absorptive power, for the water absorption subsequently obtained followed more or less the same trend whether the oil vapor was cut off or kept on continuously.

If we accept the general view that water-absorption is a direct measure of transpiration and that the rate of the former is governed by that of the latter, the results of the present experiments will not be in accord with those of the previous set of experiments, which showed that high vapor concentrations of ethereal oils brought about an appreciable rise in the rate of transpiration.

Consequently, there existed a doubt that a depression in water-absorption by a treated plant, due to a high vapor concentration, is necessarily directly linked with a corresponding decrease in water loss. To substantiate this statement experiments VIII and IX were then conducted with cut branches of *Schinus terebinthifolius* Raddi. following the same procedure, but in addition the samples, weighing about 5 grams each, were reweighed at the end of the experiment. By this means, the total loss of water through transpiration can be compared with the gain of water through absorption. The results of these two experiments are practically the same as those of the preceding series. The rate of water-absorption, again falls off in response to the application of high vapor concentrations of eucalyptus and peppermint oils (30.7 and 35.8 mg. per liter of air-current respectively). On the other hand, the application of low vapor concentrations of both oils (16.6 and 15.0 mg. per liter of air-current) has practically no measurable effect upon the rate of water absorption. Moreover, these results demonstrate

that, in both experiments, the water content of the treated samples, relative to the controls, is significantly decreased. This indicates that loss of water through transpiration exceeds gain of water through absorption. In other words, the water given off by transpiration is not compensated for by the small amount of absorbed water, and water-loss from the treated plant tissues must have taken place at the expense of their water content. This will, seemingly, go on until the water content reaches a low value when the transpiration rate should eventually cease.

Toxicity of ethereal oils. It has already been mentioned that high vapor concentrations of ethereal oils caused the plant samples, used in some of the transpiration experiments, to show some color changes and signs of wilting. Here again, in all the above set of absorption experiments, the application of relatively high concentrations of ethereal oils brought about visible signs of unhealthiness, discoloration and loss of turgidity of the treated samples. This may be due to a toxic action of such vapor concentrations, especially when applied over a long period of time.

The toxicity of ethereal oil vapors when applied to plants at high concentrations has apparently not been studied systematically. Detto (1903) observed that menthol vapor caused the death of a large area of leaf surface of *Syringa*. Audus and Cheetham (1940) reported that lemon oil vapors caused browning and death of large areas of cherry laurel leaves.

Such sporadic observations seem to suggest that the vapors of all ethereal oils, if applied to plants at high concentrations, may have a toxic action and produce a general disturbance of all vital processes, from which recovery is doubtful. Conversely, it seemed reasonable to suggest that, if these oil vapors be applied in low or moderate concentrations which are approximately equivalent to their concentrations in nature around the leaves of plants, they should exercise no harmful effects upon the treated plant tissues. It must, however, be borne in mind that this suggestion does not mean that low vapor concentrations exert no physiological effect on the treated plants, but that recovery from such effects should be quite certain.

The effect of some varied doses of chloroform upon the water absorption by plants. It then seemed of interest, for the sake of comparison, to test the effect of relatively low and high vapor concentrations of an anaesthetic, such as chloroform, upon the water absorption by a plant member. Experiment X was carried out with cut shoots of *Schinus terebinthifolius* Raddi. In this experiment, after three hours of treatment with 196 mg. chloroform per liter of air-current, estimations were discontinued and a current of pure air was kept circulating during the night. The following morning, after two normal absorption readings, a dose of 287 mg. per liter was tested. The results of this experiment gave the common form of curve obtained on applying low and high vapor concentrations of ethereal oils.

Discussion. From all the above experiments, it is clear that the effect of ethereal oils on a transpiring plant depends upon the concentration of their vapors in the surrounding atmosphere. Low or moderate concentrations, which are approximately equal to the vapor concentrations produced by volatilization of such oils from the surface of leaves secreting them, fail to produce any measurable effect on the rate of water-absorption. Such concentrations bring about a diminution in the rate of water-loss from the treated plant material. The chief effects due to such a treatment which may operate in bringing about this diminution appear to involve:

(a) Their effect upon the diffusion of water vapor. Experimental evidence indicates that the water molecules will diffuse less readily into a layer of air which is saturated with an ethereal oil vapor than into an equally thick layer of pure air. The oil vapor tends to increase the distance that the transpired moisture must move in order to find free-air conditions.

(b) Their effect upon the diathermancy of air to radiant heat. Experiments shows that an atmosphere of air saturated with an oil vapor exhibits a low transmitting power for thermal radiations. Theoretical considerations show that any slight fall of leaf temperature, due to the screening effect of an oil-saturated atmosphere, would have an effect on the vapor pressure of water. This would lower the rate of transpiration and be similar in its effect to an increase in the humidity of the air surrounding the leaf. On the other hand, the fall in leaf temperature due to the decreased diathermancy of the surrounding air, may be opposed by a rise of temperature due to the diminution of the transpiration rate; consequently the leaf temperature may not change significantly.

(c) Their lowering effect upon the permeability of plant tissues to the escape of water vapor through their outermost layers.

With increased vapor concentrations of ethereal oils the effects upon water absorption and the plants themselves are very striking. The absorption of water is considerably diminished and it finally becomes nil. This is always associated with signs of disorganization of the tested plant tissues. On the other hand, the rate of water-loss is at first increased, presumably, due to physical changes in the cell membranes of the plant tissues. These changes are believed to increase the permeability of such tissues, and thereby decrease the resistance of water-loss through their dermal layers. Eventually, a gradual decline in the rate of water-loss is expected, first, due to an insufficiently rapid supply and, finally, due to stoppage of supply. Transpiration always continues after water absorption has ceased and such a state is no doubt injurious, since a serious saturation deficit is developed in the plant associated with severe wilting of the leaves. These observations form another argument in agreement with the conclusion previously arrived at by Stiles (1938) that water absorption is not a simple process of

diffusion through cell membranes of the plant tissues, but it is a vital process depending on the normal functioning of the protoplasm. Furthermore, the present work proves that the uptake of water, necessary for growth and turgescence, is dependent on the vitality of plant issues whether absorption takes place through a root system or through a cut surface.

SUMMARY

1. Experiments are here reported in which transpiration and water absorption by plants treated with variable concentrations of ethereal oils were carried out.

2. Some of the plants studied were chosen from the groups that naturally secrete ethereal oils. These were *Eucalyptus rostrata* Schlecht., and *Schinus terebinthifolius* Raddi. For the sake of comparison, *Alhabi maurorum* Medic., which does not naturally secrete such oils, was also studied.

3. Eucalyptus and peppermint oils were used.

4. On applying ethereal oil vapors at concentrations within approximately the natural range, water-absorption by the treated samples was not appreciably affected, but water loss from such samples was retarded. This retardation was reversible and was believed to be due in the main to: a. Reduction of the diffusion of water vapor from the leaves. b. Reduction of the transmitting power of the surrounding atmosphere for thermal radiations. This would be associated with a reduction of vapor pressure gradient between the leaf and atmosphere. c. Reduction of permeability of plant tissues to water vapor.

5. Still higher concentrations of oil vapors had more striking effects. The change in the rate of water loss did not follow those changes in the rate of water absorption. Whereas the treated plants had a progressively falling rate of water absorption, yet they exhibited an increasing water-loss. The latter remained high at the expense of the moisture-content of the plant tissues, but eventually decreased to a low value. Absorption was shown to be a vital process dependent on the healthiness of the treated plants.

6. The effects of some doses of chloroform upon water absorption was found to be similar to those of ethereal oils.

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THE MORPHOLOGY AND CYTOLOGY OF LEMANEA AUSTRALIS ATK. (Concluded)[1]

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Auxiliary cells, to which the zygote nucleus migrates, do not occur in *Lemanea* as they do in some genera of the Nemalionales, but numerous nutritive cells are formed from the sterile laterals of the carpogonial branch and at the tips of developing gonimoblasts. These nutritive cells first make their appearance at the tips of the developing gonimoblasts and at the tips of the sterile laterals prior to fertilization, and their number is generally increased as the cystocarp develops (figs. 6, 29, 32, 33). These cells stain more deeply with haematoxylin, and their cytoplasm is generally shrunken away from the terminal wall. The single nucleus remains intact within the nutritive cell.

The zygote nucleus in *Lemanea* divides within the carpogonium, so that no true auxiliary cells are present, as noted above. The gonimoblasts originate directly from the fertilized carpogonium. Figures 29 to 31 show the beginning of this process. The chromosomes at the metaphase of the first division of the zygote (fig. 29) are too minute and too closely aggregated to be counted with accuracy, but no convincing evidence of reduction division was seen in any of the specimens available. The gonimoblasts continue to grow and branch out on all sizes, undergoing rapid nuclear and cell division (figs. 31 & 32); their growth is apical. Soon the filaments penetrate among and overgrow the cells of the sterile lateral branches (figs. 32 & 33). The cells of the gominoblast filaments are easily distinguishable from the sterile lateral cells by their very large nucleoli and by their more dense cytoplasm. The cells of the sterile laterals are generally very vacuolate at this stage.

When the gonimoblast filaments have become about five or six cells long, a migration of nuclei toward the carpogonium is initiated in some of the filaments (figs. 9, 33 & 34). The beginning of this migration is seen in figure 33. In all of these illustrations it will be noted that the very much enlarged pit-connections are ruptured and dislodged by the nuclei as they move from one cell to the next. This may be best seen in figures 9 and 34 in which it is apparent that a considerable amount of cytoplasm is also flowing towards the base of the cystocarp. The sterile laterals manifest no nuclear migration, but remain intact. The hypogynous cell and the cells attached to it retain their nuclei, and their pit-connections persist unaltered. The end result of this cellular fusion is the formation of a sort of placental cell, such as

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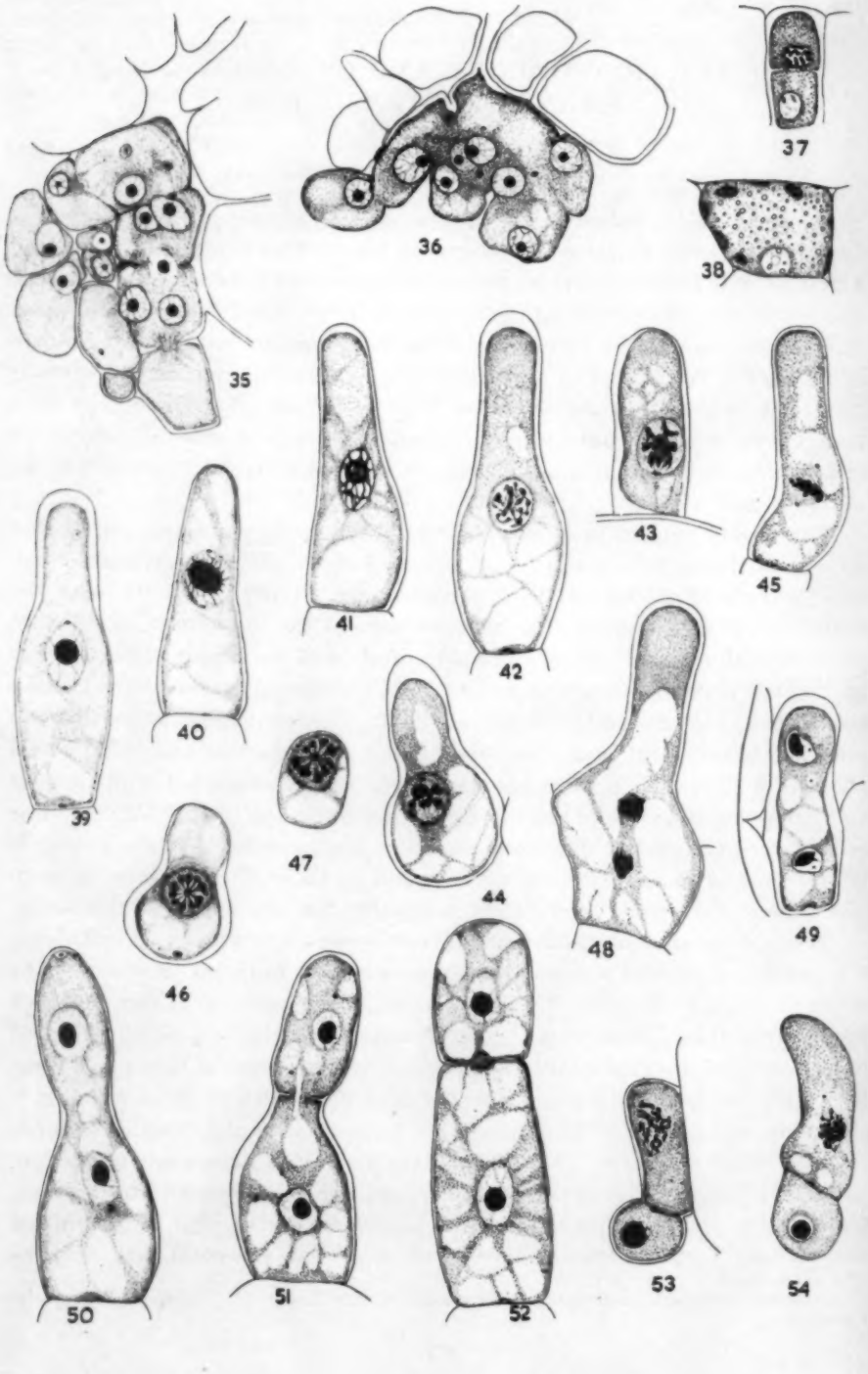
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Svedelius (1933) has reported for *Asparagopsis armata,* the only difference being that the hypogynous cell is not here involved. Figures 35 and 36 illustrate the last stages in the development of the placental cell; at this stage, the cystocarp is clearly differentiated into a gonimoblast-placenta and sporogenous (carpospore-forming) filaments.

The further growth and transformation of the cells of the gonimoblasts into mature carpospores are accomplished over several months. The filaments grow apically, and it is here that mitosis may be studied to best advantage. As the carpospores mature, their walls thicken to form the two-layered structure to which reference has previously been made. At the same time, a mucilaginous sheath envelops them, and the cytoplasm and yellowish-green pigment become concentrated around the single nucleus. Distinct plastids are not present, but large amounts of Floridean starch may be demonstrated in the spores by means of the iodine test.

In the very latest stages of cystocarp formation sterile filaments or paraphyses may originate from the placental cell. The production of these filaments often continues late into the spring, and is more pronounced in some thalli than in others.

A transverse section of a mature sexual shoot is shown in figure 10. It will be noted that the entire interior of the thallus is filled with maturing carpospores. The central axis is abundantly supplied with entwining filaments. As the season progresses with attendant decrease in rainfall and water level, the mature carpospore-filled sexual thalli are left exposed on the rocks of the stream bed. Although they may be alternately dried and immersed with variations in summer rainfall, germination of the carpospores is not initiated until immersion in very cold water the following winter. No provision for spore dissemination, other than fragmentation of the thalli, is apparent.

Cytological considerations. Cell structure. Pit-connections form a very important feature of the cell structure in *Lemanea.* They are prominent in

FIGS. 35–54. Camera lucida drawings of *Lemanea australis.* FIG. 35. Late stage in formation of placental cell; sterile cells still intact. × 600. FIG. 36. Mature placental cell. × 600. FIG. 37. Ten late-prophase chromosomes in one of the pseudo-parenchymatous cells of the cortex. × 1225. FIG. 38. Medullary cell of the cortex treated with iodine to show the Floridean starch granules. × 1225. FIG. 39. Early prophase. × 1225. FIG. 40. Desoxyribose nucleic acid flowing out from the nucleolus. × 1225. FIG. 41. Later prophase. × 1225. FIG. 42. Distinct chromatin bodies forming. × 1225. FIG. 43. First appearance of spindle fiber attachments. × 1225. FIG. 44. Advanced prophase stage. × 1225. FIG. 45. Lateral view of metaphase. × 1225. FIG. 46. Polar view of metaphase; note ten chromosomes and central centrosome. × 1225. FIG. 47. Polar view of early anaphase. × 1225. FIG. 48. Early telophase. × 1225. FIG. 49. Late telophase. × 1225. FIG. 50. Nuclear division completed; note constriction of elastic wall and vacuolate cytoplasm. × 1225. FIG. 51. Beginning of cytokinesis; note centripetal furrow. × 1225. FIG. 52. Late cytokinesis; wall formed. × 1225. FIG. 53. Diakinesis-like chromosomes in early gonimoblast filament. × 1225. FIG. 54. Probable early meiotic prophase. × 1225.

all three successional forms of the plant (figs. 16, 19 & 34), and they are very useful in the study of ontogeny, because they indicate cell lineage. The size of the pit-connection in *Lemanea* is directly proportional to the size of the cell. Furthermore, considerable variation in their structure has been observed. Study of this feature of *Lemanea* would seem to indicate that the diverse opinions as to the structure of the pit-connections among the various species of Florideae might all be verified in each species individually, if it were studied under diverse conditions and in different parts or different successional forms of the same plant.

In living plants the pit-connections appear to be two closely apposed lenses which are surrounded by a clear hyaline area (figs. 17, 20 & 21). The use of phase equipment failed to reveal any distinct membrane between the lenses. Only in stained specimens can a delicate membrane be discerned from time to time. Methyl green has been an effective tool for demonstrating this membrane in the Chantransia-stage, but it may also be perceived in some haematoxylin preparations, as a scrutiny of figures 31 and 32 indicates. Figures 33 and 35 show that the haematoxylin-positive lenses are indeed surrounded by a hyaline zone which, in turn, is bordered by a dense chromophilous ring, as Kylin (1940) has reported. Célan and Mangenot (1939) state that the chromophilous ring is lipoidal in nature, but no effort has been made to substantiate this statement, beyond observing that the ring is regularly blackened by osmic acid fixatives. In *Lemanea*, true plasmodesmata may be seen passing through the lenses in some instances. That there is protoplasmic continuity between the cells of the cystocarp, seems true beyond all doubt. The function of the nutritive cells in these structures depends upon this continuity, and, as a matter of fact, the continuous strands of protoplasm can be seen microscopically. This continuity becomes more pronounced as the gominoblast nuclei begin to migrate towards the future placental cell, and when they push the pit-connections to one side during their migration.

Mature vegetative cells of *Lemanea*, especially those of the outer cortex, contain a number of discoidal and branched plastids which lie in the peripheral layer of cytoplasm. Special attention was devoted to a study of plastid ontogeny in living, meristematic regions of *Lemanea* in view of long continued disagreement among cytologists as to the origin of these cell organelles. Their ontogeny was followed in germinating carpospores, chantransial filaments, apices of sexual shoots, in the developing sex organs and in the gonimoblasts. Direct observations of these living tissues offers no conclusive support for the theory that the pigmented plastids of *Lemanea* develop from either proplastids or chondriosomes. On the contrary, plastid development apparently occurs by progressive localization of diffuse pigment in successively older cells, in much the fashion that it is reported by

Stone (1932) to occur in leaf cells of potato. These pigmented denser regions of the cytoplasm are the plastids, which undergo segmentation in mature cells to form discoidal or ribbon-like bodies. In the description of the maturation of the carpogonial branch, one of the changes noted was a disintegration or disappearance of the plastids particularly in the carpogonium; while living and stained Meves and modified-Benda fixations of this phase revealed the presence of various granules in the carpogonium, no conclusive evidence was obtained for their genetic relation to plastids, as described by Mangenot (1922).

Figure 38 represents a subsurface cell of the cortex which has been stained with iodine. The small granules distributed throughout the cytoplasm are apparent only after this treatment, and they are brick red in color, while the plastids remain a pale green. These granules, which may be demonstrated in almost any part of the plant, are the Floridean starch granules which represent the storage form of excess photosynthate in *Lemanea*. Tests for simple sugars on rapidly growing sexual shoots yielded only negative results.

With the exception of the placental cell of the cystocarp, all the cells of *Lemanea* are uninucleated. Nuclei in the vegetative cells are generally parietal in location and from 4.5 to 5.5 microns in diameter. In the cystocarp cells, the nuclei are usually centrally located, and show what may be interpreted as haploid and diploid difference in size. This size difference is most obvious in the nucleoli which, as in Rhodophyceae generally, are very prominent. Two nucleoli frequently appear in the cells of the gonimoblast filaments; however, these are approximately half the size of the single nucleolus. It is probable that the latter is formed by the fusion of two nucleoli, although the fusion has not been directly observed. Living nuclei are optically empty except for the nucleolus.

Faint chromatic threads may be seen radiating from nucleoli of stained interphase nuclei (figs. 32 & 35). That these threads are not composed of desoxyribose nucleic acid, is evidenced by their negative reaction in Fuelgen preparations. It is very clear that in *Lemanea*, all of the desoxyribose nucleic acid is localized on the nucleolar surface (figs. 30 & 31). Critically differentiated haematoxylin preparations consistently give this picture. The Feulgen technique was used to verify this observation, in view of the suspicion with which "karyosome nuclei" are currently regarded in cytology. The Feulgen technique reveals a very definite variation in the desoxyribose nucleic acid content of *Lemanea* cells; a very small amount of the acid is present in vegetative cells. The nucleolus of *Lemanea* appears to be a dual structure, an amphinucleolus, with the desoxyribose nucleic acid absorbed upon the Fuelgen-negative phase. Figures 30, 31 and 32 show that the amounts of these components may vary considerably from cell to cell, and

this would seem to have some relationship to the desoxyribose and ribose nucleic acid cycle in this plant.

Mitosis and cytokinesis. The apical cells of well-developed gominoblasts proved to be the most favorable place for studying nuclear and cell division. The relatively large size of their nuclei and rapid proliferation of the cells make the mitotic process fairly easy to follow in these structures. But even here, mitotic figures are not as plentiful as they are at the meristematic regions of higher plants. Mitosis is a rapid process in *Lemanea;* a careful scrutiny of a sexual shoot, that has grown a full inch within the space of a week, may reveal no mitotic figures whatsoever. It has been clearly established in this investigation that nuclear and cell division occur mostly at night. Sexual shoots fixed in the field at 2 a.m. show the greatest number of mitotic figures. According to Bold (1951) nuclear division in fresh-water algae is most abundant at night.

Mitosis in *Lemanea* appears to follow a normal course, although the organization of the interphase nucleus is somewhat unusual. During interphase, as noted above, very lightly staining threads may be seen passing from the nucleolar surface to the nuclear membrane. The beginning of prophase is first suggested by the appearance of two centrosomes at opposite poles of the nucleus. It has not been possible to determine the exact origin of these bodies in *Lemanea.* Figure 39 is an illustration of the earliest mitotic stage recognized in the available material. As prophase continues, desoxyribose nucleic acid progressively flows out from the surface of the nucleolus in a centrifugal direction (figs. 40 & 41). By the time that the nucleolus is no longer visible, the nuclear cavity contains lightly staining masses of chromatin (fig. 42), but no spindle fibers are evident as yet. The attachment of the spindle fibers to the chromosomes occurs at a stage in later prophase, when the double chromatid structure of the chromosomes is most evident. Figure 43 shows this stage, while figure 44 is the latest prophase that was observed.

The nuclear membrane has completely disappeared by metaphase (figs. 11 & 45); by this time, the centrosomes are very prominent structures. Figure 46 is a polar view of metaphase: ten distinct chromosomes can be counted, attached to the central centrosome by their fibers. These chromosomes separate into their component chromatids which begin to disjoin as they enter early anaphase. Figure 47 is a polar view of very early anaphase, while figure 48 shows a later anaphase stage. In metaphase, anaphase and early telophase the chromosomes are grouped in a distinct ring (figs. 29, 46 & 47). This ring effect is perhaps best shown in figure 29, which is a metaphase plate in the zygote. Here the chromosomes are too small to be counted distinctly, but there appear to be between eighteen and twenty of them.

Telophase is manifested by a complete clumping of the chromosomes, so that there is no longer a possibility of making counts. The chromosomes at

each pole resolve themselves into an ovoid pronucleolus which has lightly staining threads radiating from it like those noted in early prophase and the interphase. Figure 49 shows centrosomes still present at the late telophase, as well as the new nuclear membranes which appear at this time. It has not been possible to determine the ultimate fate of the centrosomes in dividing cells of *Lemanea*.

The vacuolate nature of the cytoplasm, which is shown in all of the gonimoblast cells undergoing mitosis, is very constant; it is quite possibly related to the fact that there is considerable delay between the completion of nuclear division and the initiation of cytokinesis (figs. 49 to 51). Figure 50 shows a binucleated gonimoblast cell just prior to cytokinesis; vacuoles are prominent here.

Cytokinesis in *Lemanea* is initiated by centripetal growth of surface furrows; growth of the cell wall is also centripetal. This is shown in figures 51 and 52. A superficial ring-like furrow develops centripetally in the cytoplasm, quite independently of the wall of the mother cell, although the elastic nature of the latter makes it constrict slightly as the furrow forms. A transverse wall now grows inwardly following the path of the furrow. The pit-connections at this stage appear to be only dense concentrations of cytoplasm at the region where the furrow stops its centripetal progress (fig. 52). No membrane can be discerned between the lenses of the pit-connections at this time. The pits are not clearly visible in older chains of carpospores; there seems to be a delay in the development of the lenses. This is somewhat analogous to the retarded development of polar nodules in the heterocysts of the filamentous Myxophyceae. Protoplasmic continuity is severed during the development of these distal gonimoblast filaments, and this severance is undoubtedly correlated with the circumstance that the carpospores which develop from these filaments will eventually function as individual cells.

Meiosis. As stated previously, no evidence was obtained in the present investigation indicating that meiosis occurs at the division of the zygote nucleus in *Lemanea*. On the other hand, there is incomplete direct evidence that meiosis may occur later in the young primary gonimoblasts. The nuclear divisions, which are here *tentatively* interpreted as suggesting meiosis, occur after the primary gonimoblasts attain a length of from four to six cells. Figures 53 and 54 suggest two distinct meiotic stages, one the early prophase and the other diakinetic chromosomes. It will also be recalled that there is a very distinct difference in the size of the nucleoli in mature cystocarps. Figures 31, 32 and 33 show that there are three distinct sizes of nucleoli in the nuclei: first, the smallest nucleoli of the haploid carpogonial branch and sterile laterals; second, the somewhat larger carposporic nucleoli at the tips of the filaments; and third, the largest nucleoli in the presumptive diploid cells in the primary gonimoblasts. These observa-

tions are included herewith tentatively; obviously, this phase of the subject requires further study. The fact that approximately ten chromosomes are present during mitosis in the apical cells of older gonimoblasts as well as in nuclei of vegetative cells of the sexual shoot (fig. 37) and spermatia (fig. 28), indicates that meiosis must occur at some time between fertilization and formation of the carpospores; the exact locus of this process has not yet been determined with certainty.

Discussion. This investigation has shown that *Lemanea australis* Atk. is indeed a primitive member of the Nemalionales. Its primitive nature may be inferred from the ability of the prostrate form to survive under the most adverse environmental conditions, from the high degree of development of both the prostrate and erect phases of the heterotrichous habit of growth, and from the lack of true auxiliary cells as well as tetraspores. Since current systems of classifications of Florideae are based largely on the last two morphological criteria, these must be considered to be most important in any estimate of the position of *Lemanea* among the Nemalionales.

In his original description of the species *Lemanea australis* Atkinson (1890) remarked that the species is subject to great variation dependent upon the nature of the stream in which it occurs. This variation appears to be mostly a matter of the diameter of the sexual shoot as well as the degree of undulation between the "nodes" and "internodes." There is also considerable range in the color of the plants. They are very definitely green when young, and tend to remain so upon drying, but, as they age, there is a tendency to blacken when dried. This is a very flexible criterion, the more so, because stream conditions can modify the percentage of pigments in the plants. It is not unusual to have the plants turn from an olive-green to a brilliant red, when they are left standing in the laboratory over night. On the other hand, the form of the chantransial filaments seems to be a fairly constant feature of the species. While it has been a common practice, in studying plants from the general locality of the type specimen, to label as *Lemanea australis* all specimens of the sexual shoots that agree with Atkinson's original description of that stage, the local plants, with their aberrant chantransial filaments, show that this practice may result in confusion.

Certain features in the reproductive cycle of this plant are especially deserving of attention. It has been observed that *Lemanea* has a type of carpospore germination that is quite different from that believed to be typical of the Nemalionales (Kylin 1917). The carpospore is not liberated from the carposporangial wall, but remains within it, and develops in bipolar fashion in the manner typical of higher Florideae. In spite of this it seems best to refer to the asexual reproductive cells as carpospores rather than as carposporangia.

Rosenberg (1935), as noted above, reported the germination of carpospores of *Lemanea torulosa* in laboratory cultures; here drawings of the

Chantransia-stage, which resulted from this effort, do not coincide with the writer's observation of similar stages in the local plants. The latter's experience with carpospores indicates that they require a period of rest and prolonged cold treatment before they are ready to germinate normally.

The present study of the gross morphology of the sexual shoot of *Lemanea* is in essential agreement with the findings of Atkinson. *Lemanea* is a complex uniaxial type of plant whose basic organization, derived from transverse divisions of an apical cell, is fundamentally similar to such simpler filamentous types of Florideae as *Batrachospermum* and *Rhodochorton*.

Atkinson uses the term "procarp" to designate the carpogonial branch together with its sterile lateral branches. This, of course, is not in strict agreement with modern terminology, which reserves the term "procarp" for intimate combinations of a carpogonium and auxiliary cells (Fritsch, 1945a). While the sterile lateral branches are nutritive in function, and have very definite "Nahrzellen," they are in no sense true auxiliary cells, for the zygote nucleus never migrates into them, or is there any evidence that they play any direct part in the production of gonimoblast filaments; finally, they do not participate in the formation of the placental cell.

Lemanea would seem to be more advanced than other Florideae, if theories of trichogyne evolution are correct. Svedelius (1917) holds the view that the carpogonium started its existence as a two-celled structure, and hence he interprets the persistence of the trichogyne nucleus as a primitive condition. Yamanouchi (1906) reported a trichogyne nucleus for *Polysiphonia violacea* (Roth) Grev., and Svedelius (1915) observed a vestigial nucleus in the trichogyne of *Scinaia furcellata*. After examining hundreds of specimens, Cleland (1919) could not find a single case where a nucleus was even doubtfully present in the trichogyne of *Nemalion multifidum*. Investigation of fixed and stained as well as living trichogynes yielded no evidence whatever that *Lemanea* possesses a trichogyne nucleus, and so, if Svedelius' hypothesis be correct, *Lemanea* is no longer primitive in this respect.

The carpogonial branch of *Lemanea* is of special interest because of the opportunity it offers for the observation of the origin of plastids. There are three different major views as to the origin of these organelles: the first holds that plastids arise from localized aggregations of pigmented cytoplasm; the second traces the origin of plastids to special proplastids in embryonic cells; the third emphasizes the genetic continuity between plastids and chondriosomes. It has been stated above that the writer's observations of the process of plastid formation in *Lemanea* support the first view as to plastid development, for the process is similar to that described by Stone (1932) for potato.

The term "cystocarp" is not always used with the same connotation by

students of the Florideae. Oltmanns (1922) was inclined to the view that it should be reserved for those carposporic fructifications which are enclosed in a sterile pericarpal sheath. Others use it for fructifications lacking this sterile wall. The fructification of *Lemanea*, unlike that of most other genera of the Nemalionales, grows inwardly toward the axis rather than toward the exterior of the plant. The cortex of the plant protects the fructification; however, the appearance of the sterile paraphyses at a late date in the development of the plant and their origin from the placental cell at the base of the gonimoblast filaments, may in part justify the denomination of the fructification of *Lemanea* as a cystocarp. Moreover, Martin's (1939) application of the term to the fructification of *Chaetangium saccatum* (Lamour.) J. Ag., which lacks a sterile wall, as well as Svedelius' (1942) contention in regard to the use of the term for *Galaxaura*, seem to make this usage acceptable in the present instance.

It has been stated previously in this paper that the spermatium is uninucleated at the time of its liberation from the spermatangium. Drew-Baker (1951) considers it doubtful that the spermatial nucleus never enters a resting condition, as some have maintained; nevertheless in *Lemanea* the nucleus always appears to be in prophase when the spermatium is liberated. Kylin (1917) showed that the spermatial nucleus of *Batrachospermum* divides soon after it makes contact with the trichogyne. Cleland (1919) reported a similar phenomenon in *Nemalion*. There can be no doubt that this also occurs in *Lemanea*, as noted in the present observations. Wolfe (1904) and Cleland (1919) both maintain that this division makes the spermatium the homologue of an antheridium. While this conclusion seems reasonable enough, it does not seem to have been widely accepted.

It was pointed out above that the interphase nuclei of *Lemanea* show faint chromatic threads radiating from the surface of the nucleolus, but that these are Feulgen-negative. The desoxyribose nucleic acid, furthermore, surrounds the Feulgen-negative inner core of the nucleolus as a sheath, and it migrates centrifugally during prophase. This condition should not be confused with the findings of Geitler (1935) and Doraiswami (1946) in *Spirogyra*, nor with those of Svedelius (1937) in *Lomentaria*. *Lemanea* does not have a "karoysome nucleus," for the chromosomes are not formed from the nucleolus. This evidence is in substantial agreement with Westbrook's (1935) report for meiosis in the sporangia of higher Florideae, although she found no flowing out of the chromatin from the nucleolus. The nucleolus of *Lemanea* is a double structure: the desoxyribose nucleic acid is aggregated on the surface, as Feulgen procedures prove. It is possible that this type of organization may indeed be paralleled in numerous other cases, in which chromosomes have been said to take their origin from the nucleolus, which have led to so much confusion in the past. Latter

(1926), for example, may have been faced with this situation in *Lathyrus odoratus*, and Dangeard (1927) may have seen it in *Bangia* and *Porphyra*.

Drew-Baker (1944) considers the terms "haplobiontic" and "diplobiontic," which were first introduced by Svedelius (1915), as no longer adequate to express the complexity of morphological and cytological development that may occur in the Rhodophyceae. She has suggested that instead of speaking of "generations," we speak rather of "phases." The advantages of this terminology is clear enough in the case of such polyphasic plants as *Spermothamnion Turneri;* in *Lemanea*, however, the terminology of Svedelius, especially as he has clarified it in a later paper (1931), seems adequate. If we consider the cystocarp to be an integral part of the sexual shoot, then *Lemanea* is best characterized as a diplohaplont haplobiont, as is, for instance, *Liagora tetrasporifera*. This, of course, presupposes that the writer's hypothesis, in regard to the occurrence of meiosis in the gonimoblast filaments, is correct.

Kylin (1937) listed the occurrence of zygotic meiosis as one of the attributes which serve to separate the Nemalionales from the higher Rhodophyceae. This criterion has been retained by such authorities as Fritsch (1945a) and Smith (1950). The view that zygotic meiosis is indeed characteristic of most members of the Nemalionales is based, however, as already noted, on very limited evidence. Drew-Baker (1944), in her review of the nuclear and somatic phases in the Florideae, has pointed out that there is considerable variation with respect to the sequence of somatic phases in the Nemalionales. The tentative hypothesis that has been advanced in this paper as to the occurrence of meiosis, adds to this variation, and tentatively places *Lemanea* in a series that culminates in *Liagora tetrasporifera* and *Helminthocladia Hudsonii*. In these last two species, tetrasporangia are formed at the tips of the gonimoblast filaments at the site where carpospores are ordinarily produced in other species of the respective genera. While meiosis has not yet been observed in the tetrasporangium of these plants, its occurrence there is not at all unlikely. *Lemanea*, as noted above, forms no tetraspores, but the possibility of the occurrence of meiosis in the primary gonimoblast filaments would certainly indicate an evolutionary trend in that direction.

SUMMARY

1. The prostrate form, Chantransia-stage and sexual shoot of *Lemanea australis* Atk. have been studied morphologically and cytologically in both the living and fixed and stained condition. The plants used in this study were collected from Richland Creek near Nashville, Tennessee. Herbarium specimens of these plants have been deposited in the Herbarium of Vanderbilt University.

2. The carpospores exhibit a bipolar type of germination pattern, but differ in their germination from other Florideae.

3. The sexual shoot is an outgrowth of the Chantransia-stage. The plants are homothallic; both male and female reproductive organs are borne upon internal, peripheral, generative filaments.

4. The sexual shoot of *Lemanea* is a complex uniaxial type of plant, which arises by the transverse divisions of an apical cell and further division of its derivatives.

5. *Lemanea australis* is a diphasic organism whose haploid number of chromosomes is ten.

6. The spermatium is liberated when its nucleus is in prophase, and the division is completed when the spermatium makes contact with the trichogyne. The spermatium appears to have no distinct wall at the time of its liberation, but develops one by the time it makes contact with the trichogyne.

7. The usually bifurcated trichogyne of *Lemanea australis* has no perceptible nucleus at any stage of development.

8. No auxiliary cells occur in this plant, but there are many nutritive cells produced by the sterile laterals and the gonimoblast filaments.

9. Fertilization occurs in the carpogonium. No evidence of zygotic meiosis has been observed; there is some evidence that meiosis may occur in the primary gonimoblast filaments which are produced directly from the carpogonium by lateral branching. Further study will be required to establish this tentative suggestion. Tetraspores are not formed in *Lemanea australis*.

10. A distinct placental cell is formed at the base of the cystocarp by the backward migration of cytoplasm and nuclei from some of the central gonimoblast filaments to the carpogonium.

11. The cells of the gonimoblast filaments mature directly into carpospores; development is acropetal.

12. Sterile, elongate paraphyses are produced from the base of the cystocarp late in the growing season.

13. The nucleolus in *Lemanea* is a dual structure whose outer layer is composed of desoxyribose nucleic acid and whose inner core is Feulgen-negative. The chromosomes are not formed in the nucleolus, but the desoxyribose nucleic acid migrates centrifugally from the surface of the nucleolus to form them during prophase.

14. Plastid formation in the carpogonial branch supports the condensation theory of plastid origin, rather than the proplastid or chondriosome theories.

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BULLETIN OF THE TORREY BOTANICAL CLUB

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TORREYA

FIELD TRIP REPORTS

March 29, 1952. Point Pleasant, N. J. The attractive European widgeon was observed on its favorite pond in Point Pleasant, as well as scores of red-breasted and American mergansers at Shark River; laughing, Bonaparte's, ring-billed, and herring gulls at Wreck Pond; and baldpates, coots, and horned grebes at scattered points. An eared grebe present at Shark River only a week previous (the second record of the species for the state) was looked for but not observed. Attendance: 13. Leader, David Fables.

April 6. Appalachian Trail above Blairstown, N. J. A blustery day with a late winter aspect, including a brief snow cloud seen passing us in the valley below. Flowers were backward in their blooming and attention was given to birds as paint was applied to markers on the Appalachian Trail. A pileated woodpecker was heard, but unfortunately he did not come close enough for us to see. Chickadees, nuthatches and other woodpeckers were heard as well as juncos and kinglets, but it was a typical pre-spring walk except for the calls of the spring peeper and wood frog. Attendance: 2. Leader, David Fables.

April 12. Andover-Wallpack Ridge, Sussex Co., N. J. From Andover a gneiss area in the vicinity of Hewitt Iron Mines was visited. Hepatica bloomed profusely. The workings of the pileated woodpecker were photographed. The minerals fluorite, magnitite, and garnet were collected. On a limestone area at Springdale, hepatica, early saxifrage, and rue anemone were in bloom. Solomon's seal was just coming through the ground and a large stand of betony was in the red leaf stage. Among ferns were noted rue spleenwort, maidenhair spleenwort, Christmas fern, marginal shield fern, maidenhair fern, walking fern, and rock polypody. At Wallpack a mixed limestone-shale area containing fossils of ammonite, brachiopod, crustacea, and trilobites was studied. Only hepatica was in bloom. Here also were found walking fern and maidenhair spleenwort on the limestone and rock polypody on the shale. Also on the shale was the rather rare rock club-moss, *Selaginella rupestris*. Flocks of bluebirds and tufted titmouse were observed. Attendance: 14. Leader, Forest P. Dexter, Jr.

April 20. Farmingdale, N. J. We followed the usual route for the Spring trip. The season and the Torrey date coincided more nearly than in some other springs. The *Dicentra* was in good bloom. It seemed to the leader that there was less of it than in former years. Perhaps the numerous floods are gradually destroying it. No change could be noticed in the other plants.

The disappointment of the day was finding the Allaire State Park closed. Visitors are allowed on foot but cars must be parked out on the main road. This is a much traveled road with no good parking places and fully a half mile from the ruins. In view of Superintendent Hooper's activity in the park, presumably with a crew of men, it is hoped that another spring we may not be subjected to this hazard and inconvenience. Attendance: 22. Leader, V. L. Frazee.

April 27, Milford, N. J. Though it was apparently early for the green violet and it was not located, the other characteristic flora of the area were observed. Several species new to the list being compiled by the leader were added, including the purple cliffbrake (*Pellaea atropurpurea*). The stand of the two-leaved crinkleroot (*Dentaria diphylla*) is apparently shrinking, its location being on a too-much-traveled path. The delicateness of the flora at this season is unsurpassed by anything put forth at a later date. Attendance: 5. Leader, David Fables.

May 4. Woodlands Lake, Westchester Co., N. Y. I had intended to go over some areas where the Club had been a couple of years or more ago, only to find that real estate developments had taken over a good part of the area east of Ardsley. So it goes . . . Attendance: 7. Leader, William Rissanen.

May 16–18. Sussex County Nature Conference, N. J. The thirty-eighth annual conference was held at Sparta with Mr. and Mrs. Wallace Husk in charge of accommodations at the Manor Farm Hotel just at the end of Lake Mohawk, with the overflow housed at nearby Glen Lake Lodge and Rabbit's Retreat. Dr. H. N. Moldenske led the botanic walks. They visited Sparta glen, local areas, and the Pines, for a total of 405 species recorded. Dr. Moldenke is preparing in pamphlet form a new and revised list of the plants of the area and offered to send copies to anyone for twenty-five cents (Address: c/o Union County Park Commission, Warinanco Park, Elizabeth, N. J.).

David Fables and J. D'Arcy Northwood led the bird walks, including the local area, Culvers Gap, Lafayette, Hopkins Corners, Stokes Forest, the Pines, and Woodruff's Gap. The total list of 131 birds represented an all-time high. Outstanding species were: red-headed woodpecker, snow goose, black tern, and Florida gallinule. Jim Hawley, program manger, led a trip to the limestone quarries at Sparta. Lee Ellison reported pure calcite, graphite, pyrite, mica, and crystals of corundum among the minerals seen; described the trip through the plant; and explained the use made of the products.

An evening program by Dr. Moldenke included pictures of America's favorite wild flowers as included in his recent book. Mrs. Bert Schaughency showed colored movies of flowers and birds taken on recent vacation trips, extending our conference to Minnesota, Michigan, Virginia, and Pennsylvania. Attendance: 93. Reported by Lucy Bartholomew.

May 18. Kissena Park, N. Y. The Park Department still maintains the arboretum remaining from Parson's nursery and we were fortunate in having some of the Park men who are interested in maintaining the trees and shrubs as best they can. The foreman and his helper knew the identity of the trees and gave the group considerable help in looking over the various exotic plants. Since no replacements are contemplated by the Park Department, and the trees and shrubs die off, this area will probably disappear eventually. Much of the surrounding area has been "improved" with playgrounds, etc., and the former swamp is only a muddy ditch. The leader remembers an excellent stand of wild rice (*Zizania aquatica*) which has disappeared due to filling in of the swamp. Aside from the plants, the group was pleasantly aware of some rather uncommon warblers which were passing through, bay breasted warbler for example. Attendance: 11. Leader, William Rissanen.

May 31. Martha, N. J. We expected the Martha bogs to yield much more at this season than they did. One *Arethusa* was found. Plants of *Habenaria blephariglottis* were already up, buds of *Pogonia ophioglossoides* had formed as well as those on hundreds of *Abama* and a few *Tofeldia*. *Utricularia resupinata* remains difficult to relocate. Attendance: 10. Leader, David Fables.

June 8. Van Cortlandt Park, N. Y. The open fields, woods, and swamps in the East Wood were studied for several hours. Typical wildflowers, shrubs, trees, and birds, were observed. The J. Otis Swift memorial red oak was visited on the way home. Mr. Swift, as a leader of nature walks had made this walk popular with many people in New York city and its vicinity. Attendance: 15. Leader, Jane Meyer.

June 14–15. New Jersey Pine Barrens. At Winslow Jct., *Schwalbea americana* was seen in flower. This colony has been known for at least 74 years for there is a specimen in the Philadelphia Botanical Club Herbarium dated August 1878. Another rarity occurring with *Schwalbea* is *Potentilla arguta*, known from here since a collection dated July 1894. Many of the typical and lovely pine barrens plants flowering at this season were seen and admired here. The Blue Hole (a large pond formed by chalybeate springs, the bottom having a bluish color) was visited at Inskip on the Great Egg Harbor River. Sand myrtle and turkey beard were the most interesting plants.

In the evening we were shown kodachromes, principally close-ups of orchids of New Jersey by Dave Fables and Guy Nearing, and plants of the 1951 Mt. Washington trip, etc., by Mildred Faust. Overnight accommodations were at the Hand-Phillips bungalows at Malaga Lake.

The group went to Parvin State Park Sunday a.m. for nice views of the prothonotary warbler which nests there. A colony of *Helonias bullata* and the big specimen of Saul's oak (*x-Q. saulii*) were examined. *Itea virginica* and the fringe tree (*Chionanthus*

virginica), native in the park, were of interest. After lunch at Malaga Lake a study was made of swamp and dry sand thickets, noting contrast in species of woody plants occurring in those areas. The most unusual plant was from a swamp where a colony of Mt. Holly (*Nemopanthus mucronata*) was found. The hosts are grateful for help of various participants in identifying birds, amphibians, lichens, fungi, etc. Attendance: 18. Leader, L. E. Hand.

June 21. Llewellyn Park, West Orange, N. J. Glenmont, the home of the late Mr. and Mrs. Thomas A. Edison, was the meeting place. In a tour of the homestead we visited the large study of the inventor on the second floor. There, as throughout, the room is kept as he knew it—his well worn books, his large desk, his couch, Mrs. Edison's desk, and the family photographs. An expansive east window commands a view of the New York skyline on a clear day. One could readily understand that such an inspiring vista gave added impetus to this dreamer inventor. On the grounds, we examined unusual specimens of the sorreltree (*Oxydendrum arboreum*), Carolina silverbell (*Halesia carolina*), and the Japanese snowbell (*Styrax japonica*). A beautiful Katsura-tree (*Cercidiphyllum japonicum*) had reached a height of 40 feet.

The distinctive gardens of Mr. and Mrs. George Merck and Mr. and Mrs. Hendon Chubb were enjoyed, with 31 species of birds singing or visible en route. The bird species which attracted most attention was a family group of broad-winged hawks. The nest was placed in a fork of one of the tallest Liriodendron trees in the park, at a height of no less than 80 ft. The tree was in a glen. We viewed the nest from the rim of the glen, which offered us a good look at the two downy white young, guarded by one adult. This hawk is a great rodent eater and a valuable species to have in the vicinity. It is known to soar to great heights. Attendance: 20. Leader, Gladys Gordon Fry.

June 22. Sinac, N. J. Although Mr. and Mrs. Monachino kept the rendezvous, the rain, apparently, kept the customers away.

June 28. Roselle, N. J. A joint meeting with the American Fern Society was held in the leader's fern garden where most of the larger native ferns, including mutants and hybrids, have been successfully established. Of special interest however is the large collection of English crested varieties and Japanese ferns that have proved hardy in the Metropolitan Area. Of special interest to rock gardeners is a small fern from Chile, *Blechnum Pinna-marinum*. This only grows about four inches high and spreads quite rapidly. Attendance: 32. Leader, M. D. Mann, Jr.

June 29. Staten Island, N. Y. Upland field, salt marsh, and fresh water swamp areas were visited in a 15 mile "tour" of the Island. In addition to 20 genera and about 33 species of grasses, a large colony of *Penstemon laevigatus* and a "last remaining" stand of *Clematis ochroleuca* were found. Due to continued warm weather many of the early blooming grasses, such as the Poas, had already lost seed and were in an advanced stage, while later blooming species were at their best for identification. Attendance: 9. Leader, Robert C. Meyer, Jr.

July 27. Farmingdale, N. J. We explored the oaks at Farmingdale and saw a few exotic trees on the old Windsor Place south of Farmingdale. The site of an operation digging marl by steam shovel some seventy years ago was visited but the interest seemed more in pollywogs than in the marks of the digging. We found a few plants of *Viola Rafinesquii* still in bloom. There was a beautiful display of *Lilium superbum* along the railroad south from Farmingdale. Attendance: 12. Leader, V. L. Frazee.

Aug. 2. Buck's Hollow, Staten Island, N. Y. Of a considerable list of plants seen, the following were of most interest from point of numbers, appearance, or uniqueness to the habitat: *Lilium superbum, Smilax glauca, Veronica virginica, Cornus paniculata, Celastrus scandens, Asclepias viridiflora, A. incarnata* var. *pulchra, Scrophularia leporella, Rhexia virginica, Acer negundo, Mimulus ringens, Ludwigia alternifolia, Hypericum punctatum, Lycopus virginica, Silene stellata,* and *Rhus vernix*. Attendance: 4. Leader, Mathilde P. Weingartner.

Aug. 9. Wallpack Ridge, Sussex Co., N. J. The group was first shown bear's foot (*Polymnia uvedalia*) at its only station in New Jersey, just north of Harvey's Mill. Its general resemblance to the sunflowers was striking. The alluvial woods bordering the Delaware River yielded ostrich fern and the pale jewelweed. Riverweed (*Podostemum*

ceratophyllum) occurred on the exposed rocks of the riverbed, while *Equisetum variegatum* was observed a short distance back from the river. There were still a few blooms of the great St. Johnswort though most had gone to seed. Near Rosencranz Ferry the rock selaginella (*S. rupestris*) and ground cedar (*Lycopodium tristachyum*) were noted. The several hours afield in this region showed its great potentialities and certainly trips at other seasons in the future would be desirable. Attendance: 7. Leader, J. L. Edwards.

Aug. 10. Whitesbog, Burlington Co., N. J. Six consecutive days of rain left most of the region considerably under water, but the Franklinia blossoms seemed larger than ever as a result. Cardinal flower stood almost seven feet tall! The venus flytrap and southern pitcher plant (*Sarracenia flava*) are reproducing in Miss White's garden and appear very healthy. The group was impressed by the height of the sweet pepperbush and also by the rose-colored variety taken from a local swamp some years ago. Attendance: 4. Leader, June Vail.

BOOK REVIEWS

Wild Flowers for Your Garden. By Helen S. Hull. 280 pages; illustrated. M. Barrows & Company, Inc., New York. 1952. $4.95.

This book will not help you to identify wild flowers. You must look elsewhere for that. But even if you do not known the name of a wild flower in the field or woods it will still help you grow it in your garden if you wish to do so. It says simply and repeatedly to lift the plant with care to minimize root injury, preferably when the plant is naturally dormant, and reset it with the least delay in the part of your garden that has a similar environment—similar light and shade conditions, similar soil and moisture, and where other plants of the same type of plant community have been successfully reset. Mrs. Hull promptly makes the point that not all wild plants are easily adapted to the wild flower garden, even with this degree of care. A great contribution of her book is to give generous lists of plants which she, or some other wild flower garden in the United States, has found desirable and adaptable to a wild flower garden.

"A wild flower is a native flowering species." However, the book is intended to be useful over the whole U. S. and Mrs. Hull does not hesitate to encourage trying wild flowers in your garden that are native to another section rather than locally, provided the environment is similar. Her definition of a wild flower garden is: "A place where plants native to the United States are arranged in pleasing design and grown under conditions that suggest their natural state."

Much has appeared in print about nature preserves and sanctuaries but this book suggests that "home is a sanctuary" for "preserving our heritage." It also supports the thesis that planned new communities and housing developments would do well to restrain the use of bulldozers and the thoughtless uprooting of native plants already established.

Some ecological principles are set forth in a general way and then specifically applied to the establishment of wild flower gardens on rocks, sunny fields, woodlands, ponds, brooks, and bogs. It is pointed out that the principles are the same regardless of the size of the garden so that the small place, even in town, may have such a garden. In each instance extensive lists of plants are suggested. A chapter is devoted to ferns, to wild flowers adapted to attract birds, to windbreaks, to violets, and to the terrarium —here called a "wonderglobe."

The second part of the book describes a wild flower garden from every state. They are arranged alphabetically which certainly makes for variety if reading the book through. However, you soon become impatient and skip to your own state, to your native state, and to others which excite the curiosity. Perhaps you disagree with the choice. Lists of plants are provided and one finds as expected that certain plants are popular in several states but also there is a wide diversity in the gardens from adjacent states. For instance, the gardens of Maine, New Hampshire, and Vermont total over 30 listed species with only jack-in-the-pulpit, trillium, and violets as common to all three. You may decide to take this book with you on that motor tour and visit these people.

In the third part of the book, called "Plants to Grow," there are rather specific directions for propagation. This starts off with 12 favorites, named most often by wild flower gardeners across the country—Bloodroot, jack-in-the-pulpit, common American columbine, mertensia (Virginia bluebells), blue phlox, large-flowered trillium, trout-lily, hepatica, dutchmans-breeches, cardinal-flower, wild ginger, and crested iris. The order is that of their popularity. The following chapter has over 40 additional plants that are being successfully grown in wild flower gardens, though less generally.

The fourth and last part, "Down to Earth," is devoted to propagating skills—collecting, division, seed, and purchase. These directions and precautions will be very helpful but no more so than the chapter on soils and that on culture and maintenance. If you would like to know Mrs. Hull's idea of choice native flowering trees, shrubs, and vines, that will be found in the appendix. Here also are listed books, state and regional publications, commercial suppliers of wild flower plants and seeds, and a glossary. By this time it will be generally agreed that the author has attained her goal, "to communicate my delight in growing wild flowers for the joy that is in it." The full-page black and white photographs by Roche are very nice and we enjoyed the drawings by Alexander Seidel but the full-color plates disappointed us, or maybe we expected too much.—JOHN A. SMALL, New Jersey College for Women, Rutgers, The State University of New Jersey.

Important Tree Pests of the Northeast. (A revision of Tree Pest Leaflets Nos. 1–55.) 2nd ed. 191 pages; illustrated. Evans Printing Co., Concord, N. H. 1952. $2.00.

The "Tree Pest Leaflets," the first of which was published in Sept. 1936 on the "Eastern Spruce Gall Aphid," were the result of an effort to make available to foresters, forest owners and public officials reliable information on the various troubles affecting trees. To this end each leaflet was prepared by an expert in that particular field. By 1940, 300,000 copies had been distributed, and by 1945 the supply of the bound volume published in 1940 was exhausted.

Continued requests encouraged the Committee to produce the present second edition, which, in addition to bringing all subjects up to date, includes several new subjects issued as leaflets in 1950 and 1952. Space is saved by omitting the titles and affiliations of the various authors, a list of which, with all the accompanying details, is appended. Ample room is thus provided for other appendices, i.e., the common and scientific names of the plants mentioned, general references, an index to insects and diseases arranged according to host plants, and a general index to insects, diseases and other causes of injury.

As in the first edition, the diseases and pests are conveniently arranged in allied groups: thus, under "Insects Attacking Forest and Shade Trees," the Leaf-eating Insects, the Sucking Insects, and Borers and Weevils are grouped together; under "Diseases of Forest and Shade Trees," Leaf Diseases, Bark and Stem Cankers, Diseases of the Sap Stream, Wood Rots; under "Joint Attacks of Insects and Fungi," the Beech Scale-Nectria and Dying of Birch in the Northeast are assembled; and, finally, a miscellaneous class is appended in which are included "Ants injurious to trees and wood products," "Red spiders," (otherwise known as mites), fire damage, damage done by wild life; and valuable sections on spraying and spray materials.

Not only have all the original leaflets been completely revised, and in most cases re-written, but five new subjects published as separate leaflets in 1950 and 1952 are included. We learn that in April of this year (1952) almost 100,000 copies of reprints from this bound volume were distributed in the form of leaflets like the old ones and there are still about 40,000 copies of these revised leaflets on hand for sale to agencies who wish to buy them, at the original price of $1.00 per hundred.

With such a tremendous amount of detail it is not at all surprising that one or two slips have been made: in the Contents, under "*Wood Rots,*" White Trunk Rot of Conifers should read White Trunk Rot of *Hardwoods;* (given correctly in the text); in the leaflet on Syramore and Oak Anthracnose, p. 95. "European" sycamore should be *oriental* sycamore, the European sycamore being commonly identified with the sycamore

maple, *Acer pseudoplatanus*. It would be better, indeed, in order to avoid this confusion, to say *oriental plane*.

This reviewer feeds that this new edition with its wealth of up-to-date information thus carefully arranged can not be prased too highly; in fact it is difficult to find words to express adequately its great value to foresters, land owners and all tree lovers. The Committee of the Society of the American Foresters, in particular its Chairman, Dr. H. I. Baldwin, Director of the Fox Experimental Forest at Hillsboro, New Hampshire, are to be congratulated not only on this splendid addition to the literature of forestry, but also for making available to any interested person this treasure-chest of accurate and latest popular information.—A. H. GRAVES.

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LAZELLA SCHWARTEN

WITH THE COLLABORATION OF THE EDITORS OF THE TAXONOMIC INDEX

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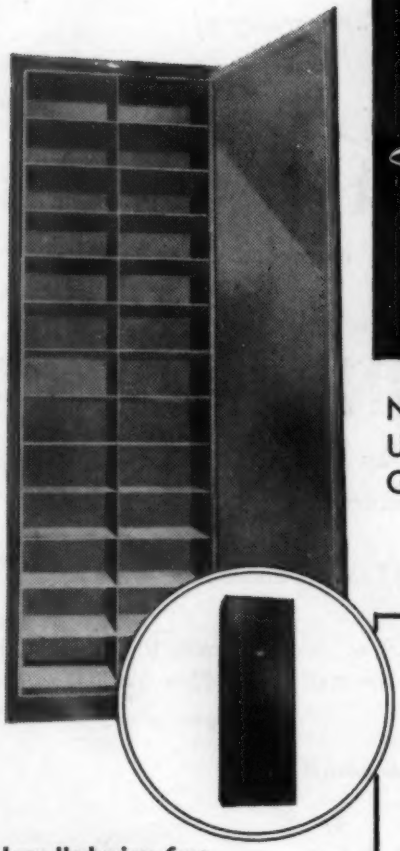

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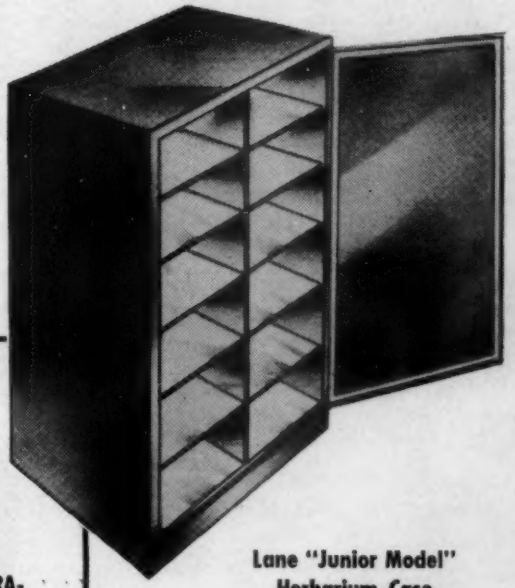

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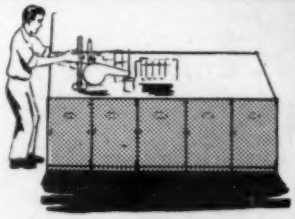

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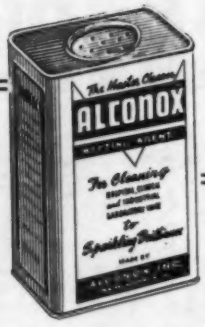

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